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# 1.

## *Paradilepis simoni* n. sp., a Cestode Parasitic in the Osprey. (Cestoda: Dilepididae).[1]

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(Text-figure 1).

The knowledge of helminths parasitic in North American birds is very incomplete, especially for the region west of the Mississippi. Not only is this true in regard to parasite-host ecology, but a little work with almost any group of birds discloses undescribed forms or species unreported from North America, as well. In fact, anyone wishing to carry out host-parasite studies must devote considerable time to describing species—time which could be more profitably spent otherwise. The osprey might be mentioned to illustrate this situation. Of this bird the writer has examined but three specimens, one each from Ohio, Wisconsin and Wyoming. From this small series of birds, four species of helminths were collected; of these, two species were undescribed and two had never been recorded from North America. While it is true that a comparable situation is not to be expected in every case, it soon becomes obvious from work with a given host-group that much remains to be done before the helminths encountered in birds can be readily identified.

The cestodes with which this paper is concerned were obtained from the small intestine of an osprey, *Pandion haliaetus carolinensis* (Gmelin), collected on June 3, 1948, near Moran, Wyoming. This osprey was one of 267 birds collected by the writer for helminthological study from the Jackson Hole region of Wyoming.

A total of more than 75 worms was obtained. Whole-mounts were prepared of specimens stained with Semichon's acetic carmine and Delafield's haematoxylin. Serial sections, cut at 15$\mu$, were also studied.

This cestode is named in honor of Mr. James Simon, Director of the Jackson Hole Wildlife Park, whose generous cooperation contributed much to the success of the field work in Jackson Hole.

[1] Contribution of the 1948 Research Program of the New York Zoological Society at Jackson Hole Wildlife Park.

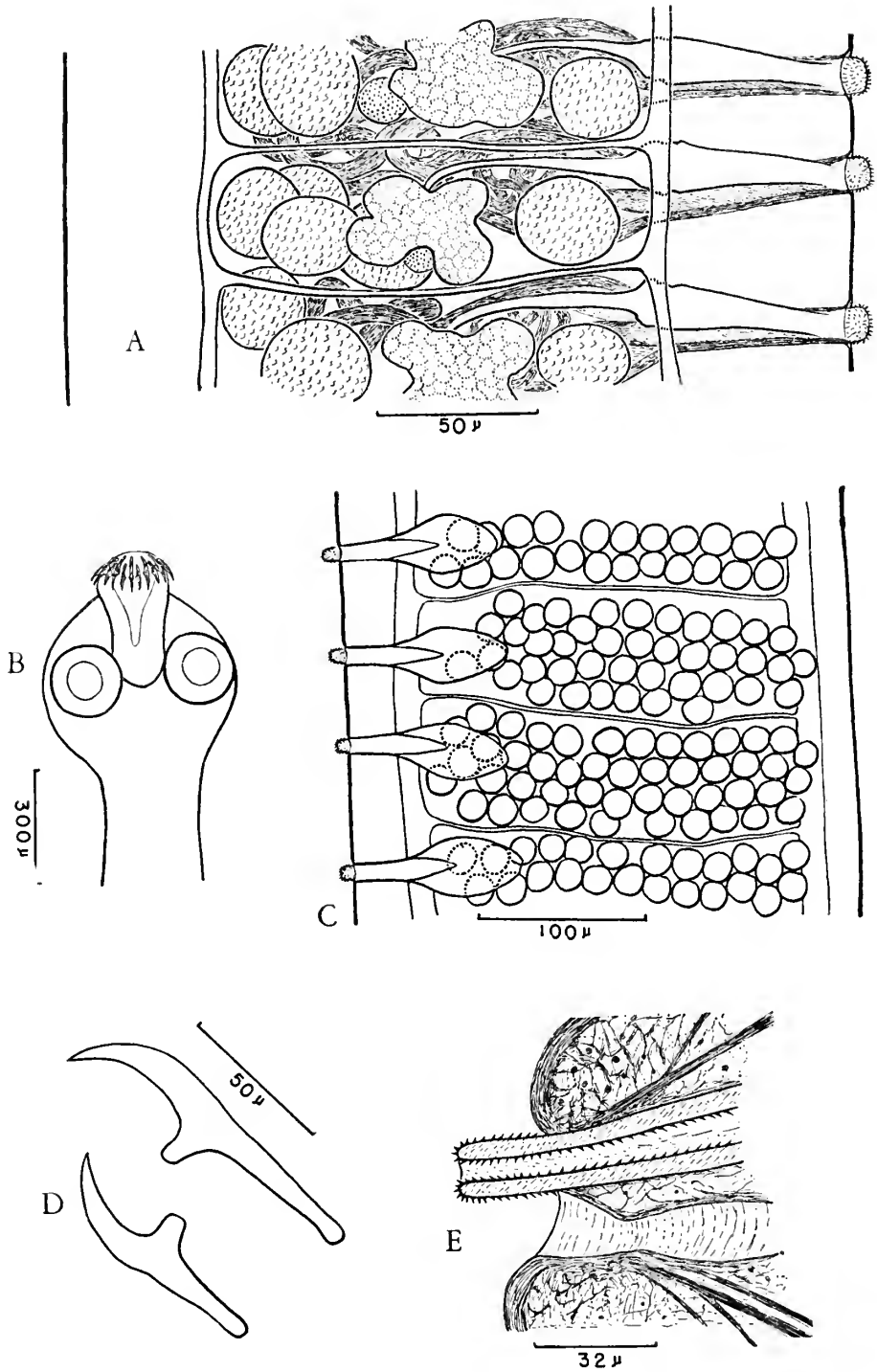
[2] Now with U. S. Public Health Service, Anchorage, Alaska.

[3] Section on Parasitology, B. B. Morgan, Project Leader.

### ***Paradilepis simoni*** n. sp.

(Text-fig. 1 A-E).

*Diagnosis*: Strobila from 50 to 90 mm. long; greatest width, up to 450 $\mu$, attained in terminal gravid segments. External segmentation absent; strobila very delicate and translucent in the living worm. Scolex large and distinct from neck; from 470 to 596 $\mu$ in diameter. Suckers from 180 to 220 $\mu$ in diameter. Well-developed rostellum slightly over 100 $\mu$ long; armed with about 36 hooks arranged in a double row. Large hooks from 98 to 102 $\mu$ long; small hooks 68 to 72 $\mu$ long. Hook shape typical for genus. Neck from 250 to 270 $\mu$ wide, narrowing gradually to a distance of about 2 mm. posterior to scolex; from this point the strobila widens to reach greatest width at posterior end. Musculature consists of two layers; the first layer, of longitudinal fibers, is from 1 to 3 bundles deep; directly beneath it is a layer of transverse fibers. Excretory canals typical in arrangement; the ventral longitudinal canal measures from 6 to 20 $\mu$ in diameter; the dorsal and transverse canals about 3 $\mu$ in diameter. Internal segmentation best recognized by the arrangement of the transverse excretory canals, which divide the strobila into about 30 "segments" per mm. of length in the mature region. Genital organs not confined entirely to space between transverse canals, but overlap into adjacent segments. Genital *Anlagen* appear about 2 mm. posterior to scolex. Genital pores unilateral and sinistral; genital atrium about 16 $\mu$ deep. Genital canals pass dorsal to longitudinal excretory canals. Five spherical to ellipsoidal testes, not all in same plane, in each segment; testes measure from 26 to 33 $\mu$ in diameter in mature segments. Usually 4 testes are aporal, and one is poral of female organs; at times 2 may be poral. Flask-shaped cirrus sac extends to middle of mature segments, or beyond, dorsal to testes; it measures from 100 to 132 $\mu$ long by 30 to 40 $\mu$ wide. Cirrus heavily spined. Internal and external seminal vesicles absent; ductus ejaculatorius coiled within bulb of cirrus sac.




TEXT-FIG. 1. The morphology of *Paradilepis simoni* n. sp. The drawings were made in part with the aid of a projector. **A.** Ventral view of a typical mature segment. **B.** Typical scolex. **C.** Dorsal view of a section of gravid segments. **D.** Hooks from rostellum. **E.** Cross-section of genital atrium region, showing relation of cirrus to vagina.

Well-developed vas deferens with numerous convolutions situated in dorsal part of segment. Cirrus sac provided with strongly-developed retractor muscles. Thin-walled vagina opens ventral to cirrus sac; it enlarges gradually, attaining greatest diameter near place where longitudinal excretory canals are crossed; it narrows after this point and runs medially to join small seminal receptacle dorsal to ovary. Ovary rather variable in shape and position; usually 4-lobed, situated near middle of segment. Spherical to ellipsoidal vitelline gland dorsal to posterior part of ovary; it increases in size toward posterior end of strobila, attaining a maximum diameter of about 40 $\mu$. Uterus develops as two lateral, spherical sacs situated ventral to ovary, and connected by a narrow neck. Gravid uterus fills entire segment; unlobed and sac-like when completely gravid. Cirrus sac and vagina persist into terminal gravid segments. Eggs, from 27 to 33 $\mu$ in diameter, are arranged in 3 to 4 rows across the segments. Embryonic hooks about 6 $\mu$ in length.

*Host*: *Pandion haliaetus carolinensis* (Gmelin) (Osprey).

*Habitat*: Small intestine.

*Locality*: Moran, Wyoming.

*Type*: Three slides of cotype material have been deposited in the Helminthological Collection of the U. S. National Museum, No. 46403.

## Discussion.

As far as could be determined, the genus *Paradilepis* Hsü, 1935, has not been previously recorded from North America. Neither has the writer discovered any record of cestodes parasitic in the osprey.

Cestodes of the genus *Paradilepis* are typically parasitic in pelicaniform birds, particularly in cormorants, *Phalacrocorax* spp. The genus *Paradilepis* was established (Hsü, 1935) for cestodes from a Chinese cormorant, with *P. duboisi* as type. Hsü also assigned *Dilepis scolecina* (Rudolphi, 1819) to the genus *Paradilepis*. According to Joyeux and Baer (1935), *P. duboisi* is identical with *P. scolecina;* consequently *P. scolecina* (Syn. *P. duboisi*) becomes type species. The examination of the original preparations of *Oligorchis delachauxi* Fuhrmann, 1909, led Joyeux and Baer (1935) to place it in the genus *Paradilepis*. It had been earlier assigned by the same writers (1930) to the genus *Dilepis* Weinland. Further study of their African material disclosed that they were dealing with two species, referred to as *Dilepis delachauxi* (Fuhrmann, 1909). As a result, a new name, *P. macracantha*, was proposed (Joyeux and Baer, 1935) for *Dilepis delachauxi* Joyeux and Baer, 1930 nec Fuhrmann, 1909.

Burt (1940) described *Paradilepis brevis* from a Ceylon cormorant, apparently without referring to the work of Joyeux and Baer (1935). It is possible that *P. brevis* is identical with *P. scolecina*.

Joyeux and Baer (1935) suggested that *Oligorchis longivaginosus* Mayhew, 1925, might also belong to the genus *Paradilepis*. This is of particular interest in connection with the present paper, since *O. longivaginosus* was collected from a white pelican from Yellowstone Park, Wyoming. Apparently this species has a single crown of hooks, instead of a double row as seen in *Paradilepis*; external segmentation also seems evident.

The number of species of the genus *Paradilepis* is at present indefinite, and must remain so until some of the material is studied further. Regardless of this situation, *P. simoni* is readily differentiated from any others previously assigned to the genus in that it possesses 5 testes in each segment, instead of 4.

Although the presence of 4 testes is considered a generic character by Joyeux and Baer (1935, 1936), we do not consider it justifiable to erect a new genus for *P. simoni* on the basis of this character alone. It is otherwise very similar to the other members of the genus. Since the previously known species have been described from pelicaniform birds, it is not strange that they are morphologically similar. If, in addition to *P. simoni*, cestodes of this genus are recorded from other host groups, a much better concept of morphological variation within the genus may be had.

It is possible that *P. simoni* is an "accidental" parasite of the osprey, and occurs naturally in cormorants. It would be of interest to examine cormorants from the colony north of Jackson Hole in order to determine whether they are parasitized by any species of *Paradilepis*. Since all the hosts are piscivorous, presumably species of fish might act as the intermediate hosts of cestodes of this genus. At present, there is no reason to doubt that the osprey is the natural host of *P. simoni*.

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# 2.

# A Contribution to the Study of North American Cestodes of the Genus *Paruterina* Fuhrmann, 1906[1].

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(Text-figures 1-12).

Two of the 16 apparently valid species of *Paruterina* Fuhrmann, 1906, have been recorded from North American birds. *Paruterina similis* (Ransom, 1909) occurs in the yellow-billed cuckoo, *Coccyzus a. americanus* (L.), and *P. candelabraria* (Goeze, 1782) is the most frequently encountered cestode parasitic in owls. The latter occurs in Europe as well as in North America, and infects several species of owls (Wolffhügel, 1900; Rausch, 1948). Evidence to the present would indicate that a high degree of host specificity has been developed in the cestodes of this genus.

It is the purpose of this paper to describe two species of *Paruterina*, and to include some remarks concerning the two previously-recorded North American species. The undescribed species were collected by one of us (R. R.) from birds in the Jackson Hole region of Wyoming. Both were taken from hosts whose parasites probably have not been previously studied.

The Wyoming birds parasitized by cestodes of the genus *Paruterina* were a rock wren, *Salpinctes o. obsoletus* (Say), and a green-tailed towhee, *Chlorura chlorura* (Audubon), which were collected from the same area, along with numerous birds of other species. The wren was collected from the southeast slope of a hill, at an altitude of about 7,000 feet. Sandstone outcroppings were numerous here, and rock wrens were rather commonly observed among them. A marmot, *Marmota flaviventris nosophora* Howell, was the characteristic mammal of this zone. The towhees were common a few hundred feet lower, where a sage, *Artemesia tridentata* Nutt., was the characteristic plant. Brewer's sparrow, *Spizella b. breweri* Cassin, was also characteristic of this habitat.

In view of the fact that representatives of the genus *Paruterina* have not been often reported in North America, it seemed unusual to collect two undescribed species from so small an area. However, since the morphological differences are quite distinct, there can be no doubt as to their specific validity. As pointed out earlier (Rausch, 1948), the helminth parasites of the North American avifauna are only poorly known.

### *Paruterina chlorurae* n. sp.

(Text-figs. 1-4).

*Diagnosis*: Strobila from 35 to 50 mm. long; greatest width, attained in terminal gravid segments, about 1 mm. Strobila consists of about 140 segments; margins of latter not serrate. Segments wider than long in mature segments, with a gradual increase in length as segments become older; terminal gravid segments, in well relaxed strobilae, considerably longer than wide. Scolex about 550 $\mu$ in diameter, not set off from neck. Suckers rather weakly developed, about 180 $\mu$ in diameter. Rostellum armed with a double row of hooks, from 40 to 42 in number; large hooks 20 $\mu$ long, and small hooks 16 $\mu$ long. Handle of larger hook about same length as guard and blade; guard of smaller hook relatively shorter, with blade and guard of nearly equal length.

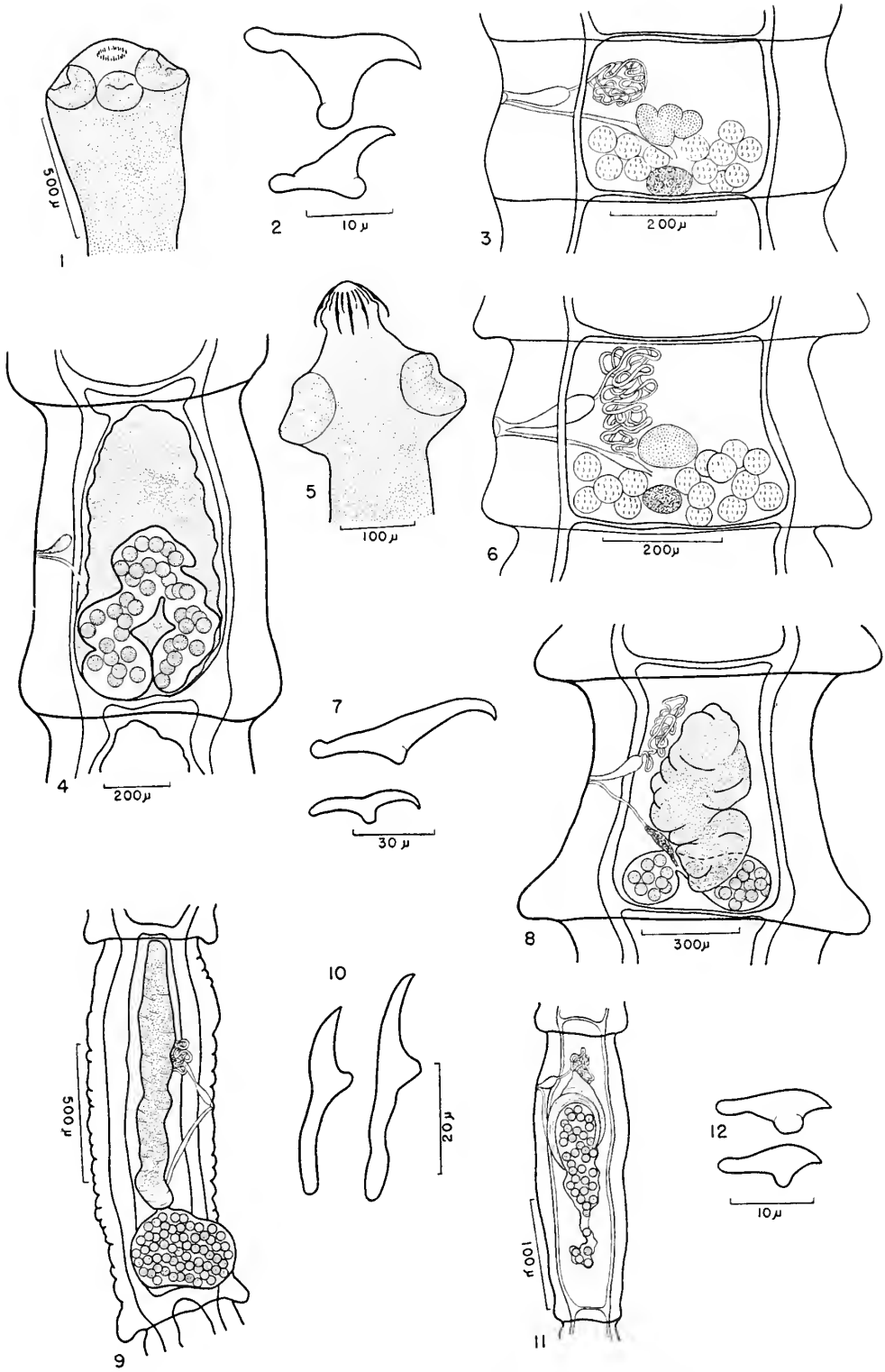
Ventral longitudinal excretory canals measure about 33 $\mu$ in diameter; dorsal canals about 10 $\mu$ in diameter, median to ventral canals. Transverse canals about 3 $\mu$ in diameter. Genital pores irregularly alternate; genital ducts pass between longitudinal excretory canals. Musculature well developed; longitudinal bundles numerous.

Cirrus sac anterior to vagina, from 105 to 119 $\mu$ long by 23 to 29 $\mu$ wide. Cirrus sac does not extend to level of ventral longitudinal excretory canal. Internal and external seminal vesicles absent. Vas deferens well developed and strongly coiled in area between poral ventral excretory canal and ovary. Testes spherical, from 10 to 12 in number; about 50 $\mu$ in diameter in mature segments. Testes lateral and posterior to female genital organs, not extending anterior to vagina on poral side, nor anterior to ovary on aporal side.

[1] Contribution of the 1948 Research Program of the New York Zoological Society at Jackson Hole Wildlife Park.

[2] Now with U. S. Public Health Service, Anchorage, Alaska.

[3] Parasitology Section, B. B. Morgan, Project Leader.




TEXT-FIGS. 1-12. **1.** Scolex of *Paruterina chlorurae* n. sp. **2.** Rostellar hooks of *P. chlorurae*. **3.** Mature segment of *P. chlorurae*. **4.** Gravid segment of *P. chlorurae*. **5.** Scolex of *P. morgani* n. sp. **6.** Mature segment of *P. morgani*. **7.** Rostellar hooks of *P. morgani*. **8.** Gravid segment of *P. morgani*. **9.** Gravid segment of *P. candelabraria* (Goeze, 1782). **10.** Rostellar hooks of *P. candelabraria*. **11.** Gravid segment of *P. similis* (Ransom, 1909). **12.** Rostellar hooks of *P. similis*.

Vagina runs directly from genital pore toward ovary; poral to latter it enlarges to form a well-developed seminal receptacle. Ovary slightly lobed, about 50 by 60 $\mu$ in mature segments; situated on mid-line near middle of segment. Vitelline gland spherical to ellipsoidal, about 20 $\mu$ in diameter; situated at posterior margin of segment on mid-line, directly posterior to ovary. Uterus appears as a crescent-shaped organ ventral to ovary; the arms lengthen until the organ assumes an inverted V-shape. In terminal gravid segments, arms of uterus become somewhat sinuous. Parauterine organ develops slowly from anterior margin of early uterus; it becomes elongate and finally attains anterior margin of segment. Spherical eggs, observed only in the uterus, measure from 43 to 50 $\mu$ in diameter.

*Host*: *Chlorura chlorura* (Audubon). (Green-tailed towhee).

*Locality*: Near Moran, Wyoming.

*Habitat*: Small intestine.

*Type*: Cotype material has been deposited in the Helminthological Collection of the U. S. National Museum, slide number 46421.

*Paruterina chlorurae* is differentiated from the other species of the genus by shape, size and number of rostellar hooks. Differentiation of this species is considered more fully under the discussion below.

### ***Paruterina morgani*** n. sp.

(Text-figs. 5-8).

*Diagnosis*: Strobila about 40 mm. long; maximum width, attained in gravid segments, about 500 $\mu$. Strobila consists of about 150 segments; margins of latter strongly serrate. Mature segments wider than long; they increase gradually in length as they become older, with gravid segments being slightly longer than wide. Scolex about 250 $\mu$ wide, distinctly set off from neck; suckers about 100 $\mu$ in diameter. Rostellum armed with a double row of 34 to 36 hooks; large hooks measure 66 $\mu$ long; short hooks measure 40 $\mu$ long. Blade of large hook, slightly longer than handle, curves downward abruptly at end; guard, near middle of hook, inconspicuous. Blade and handle of small hook nearly equal in length; guard, at middle hook, about ⅓ as long as blade.

Ventral longitudinal excretory canals about 13 $\mu$ in diameter; dorsal canals about 4 $\mu$. Transverse canals about 3 $\mu$ in diameter. Genital pores irregularly alternate; genital ducts pass between longitudinal excretory canals. Musculature well developed; two rows of longitudinal and a single row of transverse fibers occur in close contact. Longitudinal muscle fiber bundles not numerous; accurate count not obtained.

Cirrus sac clavate, anterior to vagina; it extends beyond poral ventral excretory canal, and measures from 86 to 105 $\mu$ long by 16 to 20 $\mu$ wide. Internal and external seminal vesicles absent. Vas deferens well developed and strongly coiled; convolutions fill greater part of poral half of segment, from end of cirrus sac to level of mid-line of ovary. Testes spherical, from 15 to 18 in number; about 50 $\mu$ in diameter in mature segments. Testes lateral and posterior to female genital organs; not extending anterior to vagina on poral side, nor anterior to ovary aporally.

Vagina runs directly from genital pore, without convolution, to form a well-developed seminal receptacle posterior and poral to ovary. Ovary unlobed, ellipsoidal; about 120 $\mu$ long by 80 $\mu$ wide in mature segments; situated in posterior half of segment, at mid-line. Vitelline gland ellipsoidal; about 60 $\mu$ long, situated directly behind ovary somewhat anterior to posterior margin of segment. Uterus appears as an elongate organ lying transversely in the posterior part of the segment, ventral to ovary. It enlarges gradually, and finally forms an elongate, irregular sac, situated at posterior margin of completely gravid segments. Parauterine organ grows gradually from anterior margin of uterus; it does not reach anterior margin of segment. Eggs spherical, observed only in uterus; from 36 to 43 $\mu$ in diameter.

*Host*: *Salpinctes o. obsoletus* (Say). (Rock wren).

*Locality*: Near Moran, Wyoming.

*Habitat*: Small intestine.

*Type*: Cotype material has been deposited in the Helminthological Collection of the U. S. National Museum, slide number 46422.

*Paruterina morgani* is differentiated from the other members of the genus by size, shape and number of hooks, as well as by other, less obvious details. This cestode is named in honor of Dr. B. B. Morgan, Department of Veterinary Science, University of Wisconsin.

## Discussion.

At least 18 species have been assigned to the genus *Paruterina;* of these, 2 species, *P. fuhrmanni* Baczynska, 1914, and *P. melierax* (Woodland, 1929) have been transferred to other genera. Three of the remaining species, *P. angustata* Fuhrmann, 1906, *P. guineensis* Joyeux and Baer, 1928, and *P. southwelli* Hilmy, 1936, have unilateral genital pores, and are immediately separated by this character from the species described in the present paper.

Of the North American species, *Paruterina similis* (Ransom, 1909) has been redescribed by Linton (1927). This species was placed in the genus *Paruterina* by Jones (1929). Certain morphological details of this species have never been completely described; Linton (1927, page 50) stated "There is a short rostellum surmounted by a double circle of very short hooks. Their exact number was not satisfactorily made out, but there appear to be in the neighborhood of 40 . . ." Jones (1929) examined both Linton's material, and that of Ransom, but did not give further details concerning the hooks of *P. similis*. We found that *P. similis* possesses from 50 to 52 hooks, arranged in

a double row. The large hooks measure 13 μ long, while the small hooks measure 11 μ long. They are essentially the same in form, except that the larger hooks have a larger, more rounded guard (Text-fig. 12). Our observations were made under oil immersion on hooks which had been removed from the scolices, and were lying flat on the slide.

*Paruterina chlorurae* and *P. morgani* are differentiated from *P. similis* and *P. candelabraria* by hook size, shape and number (Text-figs. 2, 7, 10, 12). It is of interest to note that the North American species can also be separated by differences in the arrangement of the parauterine organ and the uterus in the fully-gravid segments (Text-figs. 4, 8, 9, 11). In fact, differences here are more obvious than are those seen in the mature segments. It might also be mentioned here that cestodes of this genus can easily be recognized as such macroscopically, at the time they are removed from the intestine of the host, by the appearance of the gravid segments.

The remaining 11 species, widely distributed geographically, are best separated by hook characters. All of these (*P. bovieni* Hübscher, 1937; *P. bucerotina* Fuhrmann, 1909; *P. cholodkowskii* Skrjabin, 1914; *P. daouensis* Joyeux, Baer, and Martin, 1936; *P. javanica* Hübscher, 1937; *P. meggitti* Johri, 1931; *P. otidis* Baczynska, 1914; *P. parallelipida* (Rud. 1809); *P. purpurata* (Dujardin, 1845); *P. septotesticulata* Moghe and Inamdar, 1934; *P. vesiculigera* (Krabbe, 1882) all differ appreciably in hook size, shape and number.

There are also differences in testes number in most cases. Where there is overlapping of this character, hook differences serve to separate the species involved. Other taxonomic details need not be discussed here in order to separate the species described in the present paper.

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# 3.

## Behavioral Interactions in a Herd of Barbary Sheep (*Ammotragus lervia*).[1]

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### INTRODUCTION.

Studies of social behavior in animals have generally been of two types, the naturalistic field investigation and the laboratory experiment. Field studies of ungulates have been made by Darling (5) on the red deer, and Mills (10), Davis (6) and Spencer (13) on the Rocky Mountain bighorn sheep. The experimental method has produced an extensive literature on dominance relationships and aggressive behavior in many species. Collias (4) has reviewed the work on aggressive behavior among vertebrates up to 1944. Studies on dominance have been too numerous even to be mentioned briefly in the present paper.

Carpenter (2) has pointed out that the development of a science of comparative social behavior requires that the results of field investigations and those of the laboratory should be systematically co-related. He also has stated that the standards of scientific research which apply in the laboratory can and should be applied in the field. Recognizing the research potentialities of an integrated approach to animal behavior, Scott (11) recently combined systematic observation and experimentation in a study of a small flock of domestic sheep living under semi-natural conditions.

The methods and aims of the following study of a herd of Barbary sheep were suggested in large part by the work of Scott and the theoretical discussions of Carpenter (2, 3). Carpenter (2) has listed 11 types of behavioral interactions found in primate societies. It was hoped that the first six of these might be studied in the Barbary sheep. They are: 1, Interactions among adult males of organized groups; 2, among adult females of organized groups; 3, between adult males and adult females; 4, between adult males and young; 5, between adult females and young; and 6, among the young. The data were to be compared with information on the domestic sheep and the Rocky Mountain bighorn. In addition, the investigator sought to obtain data relevant to the hypothesis that *deprivation is an effective instigator of aggressive behavior.*

### THE HERD.

The Barbary sheep, or aoudad (*Ammotragus lervia*) is very distinct in appearance from all other wild sheep, its most unique features being a mane of long hairs over the fore-quarters, the length of tail and the large size of the female's horns. Its color is uniform rufous tawny. The habitat of the Barbary sheep is the arid southern slopes and foothills of the mountains of North Africa, extending from near the Atlantic seaboard to Egypt. Lydekker (8) quotes reports that the animals go about in groups of four or five and may drink as seldom as once in four or five days.

The herd at the New York Zoological Park is descended from stock brought to the Park during the years 1901-1906. No new stock has been introduced since then. During the summer of 1947 the herd consisted of four rams, four ewes and four lambs. One of the lambs was a yearling, while the others were first-season. The sheep lived on an enclosed field of about two acres. They shared the field with two elands and a zebra. Human regulation of the activity of the sheep has been kept at a minimum by the Park authorities. Under normal circumstances the herd is fed about one and one-half buckets of grain, which is spread out on a large, flat rock at about 9:30 every morning. The elands and the zebra usually feed from a box some distance away, although they sometimes wander over to the rock and feed with the sheep. The grain ration is supplemented occasionally with hay, which is placed in one corner of the field. Vending machines in the Park provide special food pellets which visitors may throw through the fence. During the warm months the sheep regularly gather at the north fence in the afternoon to receive these pellets. The sheep tend generally to avoid the two elands and the zebra. In recent years a newborn lamb was killed by the male eland, and another by the zebra.

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[1] A report submitted to the New York Zoological Society on research performed as a Summer Research Fellow of the Society during July, August and September, 1947.

The writer is indebted to his colleagues, Dr. N. E. Collias and Dr. B. F. Riess, who made many valuable suggestions and participated in the observation and experimentation from time to time. Special gratitude is due a third associate, Mr. D. Lehrman, who did most of the work with the Bristol Recorder, and who shared equally in some of the experiments. The Summer Research Fellows worked under the general direction of Professor C. R. Carpenter.

## Methods.

Casual observations were made almost daily from mid-July until mid-September, and during all hours of the day, so that a complete picture of the daily routine could be obtained. Colored dyes were used to mark the individual animals until the observer could recognize them easily by differences in appearance and behavior. The following experiments were performed repeatedly: (1) tossing of bread between pairs to ascertain relationships of dominance-subordination; (2) placing of daily grain ration in a small box to study dominance-subordination relationships in a complex herd situation, as well as to provide observations on food sharing, fighting, and related phenomena; (3) frightening of the herd to elicit leadership and timidity. These experiments were carried out from July 22 to September 13. In addition, on two days a Bristol multi-pen recorder was employed in connection with the feed box experiment to ascertain the amount of time each animal actually fed from the box. Motion pictures were taken of types of behavior which had been previously recognized and described.

The study of social relationships was limited by the fact that the age and parentage of adult individuals could not be established with certainty. Although the Park maintains complete records of births and deaths, there is no provision made for identifying individual members of herds. It was possible, however, to know three ewe-lamb relationships on the basis of observed behavior.

## Daily Routine.

The daily pattern of behavior of the herd was marked by fairly regular periods of alternating activity and rest. But this was greatly modified by changes in the weather, experimentation and marked variations in the supply of food from visitors. Usually in the early morning the sheep wandered about the field. Grazing was desultory, since other food was available. At about 9:00 A.M. the sheep generally gathered on an outcropping of broad, flat rocks situated on a hillock in the center of the field, and there they rested until 9:30 A.M., when grain was scattered on a nearby rock by the keeper. The sheep ate the grain peacefully, with very little butting or shoving. By 10:15 A.M. the sheep were either back at their earlier places on the rocks or were under a tree, where they remained until after the noon hour.

Shortly afterwards children and adults would usually begin to gather along the north fence. The movement of the sheep to the fence seemed to be associated with the size of the gathering of people rather than the hour. On days when very few people visited the Park the sheep might remain entirely away from the fence throughout the afternoon. Once at the fence, the herd remained there as long as pellets were given to them, usually until about 5:30 P.M. On hot afternoons the males made occasional trips to a nearby water hole. Here they cooled themselves by sinking down into the shallow water and rolling in the mud.

In the evening the sheep wandered and rested until dark. The lambs played actively at this time by running and leaping on the rocks. During late August and September fighting and attempted breeding occurred among the males, and most frequently in the evening. At dusk the herd gathered inside or near a shed and bedded down for the night. Sometimes the sheep moved as a group, but consistent leadership was not apparent. In general, there was much independent movement among the ewes, rams and lambs.

## Matching Tests.

The matching tests were conducted every few days from July 22 until September 13 to determine dominance-subordination interactions between individual animals. Usually the tests were made in the afternoon, when the sheep were gathered at the north fence. By supplying several willing children with bread, and placing them along the fence, it was possible to disperse the sheep so that all or most of the possible pairings could be made among the rams, the ewes and the lambs. The matching of adults and lambs, or of rams and ewes, was not attempted after the first day because of practical difficulties.

The matching test was simple. The experimenter stood at the fence and held a small piece of bread in his extended hand. When two sheep, which were not more than ten feet apart, looked in the direction of the experimenter, the bread was tossed so that it landed approximately equidistant between them. No score was recorded unless both animals moved toward the bread. The one which obtained possession of the bread by causing the other to withdraw was considered dominant. The behavior elicited in this situation was clear and unambiguous; if both sheep advanced toward the food, one *always* threatened or butted and the other *always* withdrew. Sometimes the bread landed much closer to the animal known to be subordinate. In such a case the subordinate sheep might obtain the bread, but this was usually followed by vigorous butts from the dominant animal. Often, however, a quick dash by the dominant sheep caused the other to retreat, even when the bread lay directly at its feet.

On three occasions the sheep appeared to be uniformly unmotivated with regard to the bread. Two of these days were extremely hot, and the third was marked by a morning of heavy feeding. At all other times competition was keen and sustained. The method of scoring is somewhat defective in that no scores were recorded for those tests in which only one animal moved toward the food. The assumption here is that of "no contest" and this is, of course, questionable, since the animal's lack of a positive overt response to the food might be due to the presence of the dominant animal. However, the almost per-

fect consistency of the results presented in Table I, and the agreement between these results and behavior observed in other situations strongly suggest that the method is highly valid.

In the majority of contests, dominance was decided by a sudden *twisting movement* of the dominant sheep's head in the direction of the other sheep. At this "signal" (or sign) the subordinate sheep stopped advancing. Sometimes a token butt was delivered, but seldom was a more forceful attack necessary to effect retreat. Counter attacks by subordinates occurred rarely and were *never* successful. Among the rams, the ewes and the lambs straight line dominance orders were revealed on the first day and remained almost stable during the 53-day period of testing. Only two instances of reversals occurred during a total of 272 matching tests. Although interactions between rams and ewes, and between adults and lambs, were not formally tested, it was apparent that *all rams were dominant over all ewes, and all adults over all lambs.*

The results of the matching tests are presented in Table I. The dominance order is as follows: Ram 1> Ram 2> Ram 3> Ram 4> Ewe 1> Ewe 2> Ewe 3> Ewe 4> Lamb 1> Lamb 2> Lamb 3> Lamb 4>. The attempt was to test at least twice a week every possible combination of individuals within each of the three subgroups. But this could not always be done because of the difficulty of bringing certain of the sheep together. For example, matchings between lambs were often disrupted by the sudden approach of one or more adults.

TABLE I.
Results of the Matching Tests.

| *Rams** | *Number of matchings* |
|---|---|
| 1-2 | 25 |
| 1-3 | 20 |
| 1-4 | 22 |
| 2-3 | 22 |
| 2-4 | 21 |
| 3-4 | 12 |
| 4-2† | 1 |
| 2-1† | 1 |
| *Ewes** | |
| 1-2 | 22 |
| 1-3 | 18 |
| 1-4 | 15 |
| 2-3 | 15 |
| 2-4 | 13 |
| 3-4 | 9 |
| *Lambs** | |
| 1-2 | 7 |
| 1-3 | 6 |
| 1-4 | 5 |
| 2-3 | 12 |
| 2-4 | 10 |
| 3-4 | 14 |
| *Groups* | *Total* |
| Rams | 124 |
| Ewes | 94 |
| Lambs | 54 |

* Numbers indicate sheep according to position in dominance order. Number of dominant animal precedes that of subordinate.
† Reversal.

## FEED BOX EXPERIMENTS.

The feed box experiments were intended to furnish information on social behavior in a competitive group situation. The matching tests had indicated the existence of a clear, stable relationship between any two animals which were made to compete for a small food object while in relative isolation from the other members of the herd. But it could not be assumed that these relationships would hold in all types of competitive situations, especially in those where more than two animals are interactive. Maslow (9) found that stable dominance-submission relationships which were established between monkeys by the method of paired matching tests broke down when three or more individuals were placed together.

The food incentive box was heavy and made of wood, typical of those used in the Park for the feeding of large animals. Its sides were about two feet long and about one and one-half feet high. The box was modified so that the interior sides measured 15" by 12", with the depth remaining unaltered. The interior was large enough to hold more than a bucket of grain without spilling by the feeding animals. The size of the opening was such that two adults could not feed simultaneously without frequent contact, while simultaneous feeding by three adults would result in almost constant contacts. It was hoped that food sharing, and the conditions surrounding this behavior might result as well as competition for food.

The feed box experiment was conducted 12 times. On mornings when the experiments were performed, the experimenter moved the elands and the zebra from the field to adjacent pastures. At about 9:30 or 10:00 the box was placed on the rock where grain normally was scattered by the keeper. Then the experimenter emptied one bucket of grain into the box and withdrew behind a gate about 20 yards away. The sheep were observed by means of binoculars and their behavior was recorded immediately in a note book. Usually at the end of an hour it was necessary to place more grain in the box.

The general pattern of social interaction at the feed box was similar throughout the entire series of experiments. During the series of group tests an order of dominance was formed which conformed closely to that observed during the matching tests. Rams 1 and 2 always dominated the other animals at the box during the first 15 or 20 minutes of feeding. The other sheep milled around the feed box but were not permitted to eat. *The two dominant rams ate alternately.* Whenever Ram 1 raised his head to chew or rest, Ram 2 ate from the box. As Ram 1 again lowered his head, Ram 2 usually withdrew his head. A high degree of orderliness usually characterized the feeding of these two sheep. Often Ram 2 did not withdraw until

he was threatened or mildly butted by Ram 1. In the main, Ram 1 butted and shoved Ram 2, and the latter in turn kept the other sheep from the box. Upon being forced from the box by the more dominant animal, Ram 2 might circle the box and butt all the sheep in his path.[2] After the first few minutes the other animals ceased to crowd around the box. Some of them moved to a nearby tree and others formed a wide circle about the feeding place.

When he had completed his first feeding, Ram 1 left the feeding area. Ram 2 would either leave at the same time, or continue feeding. Then Ram 3, or Rams 3 and 4 together, moved up to the box, and interactions very similar to the previous ones were exhibited. During the first 30 or 40 minutes the box was controlled constantly by a pair of rams. But after the initial feeding of Rams 1 and 2 the pairings shifted frequently due to the movements to and from the box of dominant rams. From time to time ewes and lambs attempted to feed, usually with little success. The subordinate ram of a pair did most of the butting and chasing of the other members of the herd.

During the second hour the rams spent less time at the box, and when there manifested *increasing tolerance* toward the lambs and ewes. The order of feeding among the ewes was also determined mainly by dominance status, while a lamb's ability to feed depended on the tolerance of its own ewe. Often Ewe 4 and Lamb 1 (the yearling) obtained little or no food during an entire experiment. Being of low dominance status, the ewe was excluded, and the lamb likewise because it lacked high dominance maternal protection. The experiment usually ended shortly after the noon hour, when the sheep began to move toward the north fence for pellets offered by visitors.

*Dominance.* In Table II are presented the butts and threats given and received by each sheep during the series of 12 feed box experiments.[3] Except for two instances, threats were always directed by dominant animals against subordinate ones. The butt more frequently was directed by a subordinate sheep against a dominant one. Nineteen butts, of a total of 198, fall in this category.

The data on rams in Table II indicate that the dominance-subordination relationships among these animals were somewhat less rigid and involved more behavioral interaction among individuals than in the matching tests. However, it must not be assumed that relationships at the feed box were less stable. Stability cannot be inferred from the ratio of butts given and received. Nor would a mere tabulation of instances of food sharing and food hoarding provide a valid basis for inferring dominance status. For example, Rams 1 and 2 usually ate together with little overt indication of dominance-subordination. Often they fed alternately for three or four minutes without observable conflict. But upon closer examination it could be seen that Ram 1 *permitted* Ram 2 to eat with him, and even to shove him occasionally. Over-vigorous shoving or persistent crowding on the part of Ram 2 always elicited a sharp attack from Ram 1. Exchanges of butts might be equal in number but they always ended with Ram 1 in control of the box.

Wide variations in the "social distance" between different rams are apparent. Reciprocity of aggression was relatively high between Rams 1 and 2 and between Rams 2 and 4, but Ram 3 never aggressed against Ram 1 or Ram 2, and was almost never aggressed against by Ram 4.[4] The meaning of these differences in "social distance" will become clearer at a later point in the discussion. Among the sheep included in Table II, frequencies of butts and threats decrease in almost perfect rank order. The data on ewes and lambs has not been analyzed in detail because of the low frequency of aggressions. Lambs 2, 3 and 4 are not included in the Table only because their scores on both items were zero.

*Feeding time.* Scores for feeding time were computed from the Bristol recordings of an experiment on August 11 according to the method described in the first footnote to Table III. The time score for each sheep is the number of 10-second periods during which the animal had its head in the box for two seconds or longer. In Table III individual scores are given for each of nine consecutive periods. The periods are 16.6 minutes in length. Individual totals for the whole experiment indicate a lack of positive relationship between dominance status and feeding time, although the differences between rams and ewes, and adults and lambs, are on the whole substantial. The lack of relation between feeding time and dominance status may be due to wide individual differences both in rate of food intake and nutritional needs.

For most of the sheep there is a single period during which much more feeding occurred than during other periods. This would seem to justify a comparison of the periods in which individuals made their highest scores. Such scores have been indicated in the Table by a small circle. The circles follow a line which gradually descends from left to right, indicating that time-of-maximum-feeding is closely related to the dominance order. The near-zero scores of Ewe 4 and Lamb 1 have already been discussed.

*Coordinate-feeding.* An important type of social interaction among the sheep was that of coordinate-feeding, or food sharing. The concept and the unit of measurement employed are described in the first footnote to

[2] These attacks by Ram 2 against subordinate sheep appeared to be clear instances of *displaced aggression*, and will be discussed later on in this paper.

[3] A threat is defined as an aggressive movement or pattern of movements which one sheep directs at another, but which does not end in physical contact. The typical threat consisted of a sudden lowering of the head and slight movement toward the other animal. But sometimes a mere lowering and twisting of the head composed the pattern. The object of a threat usually withdrew immediately or modified his behavior in some observable way.

[4] See footnote to Table II.

TABLE II.

Total Butts and Threats for 12 Feed Box Experiments*.

| | Threats | | | | | | Butts | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Recipients | | | | | | Recipients | | | | | |
| | Ram #1 | Ram #2 | Ram #3 | Ram #4 | Ewes & Lambs | Total | Ram #1 | Ram #2 | Ram #3 | Ram #4 | Ewes & Lambs | Total |
| Ram #1 | x | 21 | 1 | 2 | 21 | 45 | x | 42 | 5 | 5 | 15 | 67 |
| Ram #2 | 0 | x | 4 | 2 | 16 | 22 | 9 | x | 2 | 13 | 16 | 40 |
| Ram #3 | 0 | 1 | x | 8 | 11 | 20 | 0 | 0 | x | 14 | 19 | 33 |
| Ram #4 | 0 | 0 | 1 | x | 18 | 19 | 0 | 8 | 2 | x | 15 | 25 |
| Ewe #1 | 0 | 0 | 0 | 0 | 5 | 5 | 0 | 0 | 0 | 0 | 17 | 17 |
| Ewe #2 | 0 | 0 | 0 | 0 | 6 | 6 | 0 | 0 | 0 | 0 | 12 | 12 |
| Ewe #3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 8 |
| Ewe #4 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 |
| Lamb #1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 4 | 4 |

* Intermittent fighting was observed between Ram 2 and Ram 4. and between Ram 3 and Ram 4, during the second week in September. Butts exchanged during these fights have not been included in the table because on the two days that these fights occurred the experimenter was occupied with taking motion pictures. However, only one fight might be said to have ended in favor of Ram 4. This fight was between Ram 4 and Ram 2. Since these fights were associated with sexual excitement in Ram 4 the table as presented is representative of social relations *before* the onset of rutting behavior. Fighting and rutting behavior will be discussed in a later section.

Table IV. The unit of measurement is, of course, arbitrary, but it has the merits of being easily computed from the raw data and of yielding quantitative relationships which are in close agreement with observations made during 12 experiments. Table IV contains data on coordinate-feeding among the rams. Both absolute frequencies and coordinate-feeding ratios indicate that among those pairings in which the possibility of coordinate-feeding existed relatively often its frequency varied widely. The ratios are high for Rams 1 and 2 and Rams 2 and 4, and low for Rams 2 and 3 and Rams 3 and 4. Parallel differences among pairs have already been noted with regard to butts and threats. *Aggressive interactions and food sharing vary together.* But although they are associated, it would be wrong to assume that one is a primary cause of the other. Rather, both are directly related to the amount of social distance between individuals. Social distance is psychological rather than spatial, and is determined by the willingness-for-contact, or tolerance, of the dominant sheep with regard to the subordinate. Lack of unilateral or bilateral aggression between two sheep may be an indication of very low tolerance on the part of the dominant animal. Thus, on the day for which coordinate-feeding data is presented, Rams 3 and 4 were the only rams together at the box for a longer time than Rams 1 and 2 were present togther, yet the only aggression between the former individuals was a single threat by Ram 3, and the coordinate-feeding ratio was 4/25. In contrast, Ram 1 threatened or butted Ram 2 sixteen times and received three butts from the latter, while the coordinate-feeding ratio was 16/21.

Quantitative data on coordinate-feeding among the ewes was not obtained because during the experiment on August 11 one or more rams were almost always present at the box. The recorded observations of all 12 experiments show that when no ram was pres-

TABLE III.

Feeding Time Scores of Sheep in Experiment Lasting Two and One-half Hours.*

| Periods† | Ram #1 | Ram #2 | Ram #3 | Ram #4 | Ewe #1 | Ewe #2 | Ewe #3 | Ewe #4 | Lamb #1 | Lamb #2 | Lamb #3 | Lamb #4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| I | 87° | 82° | 2 | 3 | 1 | 5 | 0 | 3 | 0 | 0 | 0 | 0 |
| II | 27 | 18 | 54° | 8 | 6 | 3 | 0 | 0 | 0 | 0 | 0 | 0 |
| III | 0 | 13 | 28 | 18 | 26° | 15 | 14 | 3 | 0 | 9 | 5 | 8 |
| IV | 10 | 26 | 6 | 39° | 7 | 0 | 11 | 0 | 0 | 18 | 0 | 0 |
| V | 0 | 0 | 15 | 12 | 0 | 7 | 7 | 0 | 0 | 11 | 0 | 0 |
| VI | 9 | 9 | 28 | 25 | 14 | 22° | 13 | 0 | 0 | 21 | 4 | 0 |
| VII | 12 | 0 | 5 | 15 | 12 | 0 | 35° | 0 | 0 | 36° | 0 | 11 |
| VIII | 0 | 28 | 1 | 28 | 0 | 16 | 0 | 0 | 0 | 8 | 11° | 0 |
| IX | 0 | 43 | 19 | 19 | 15 | 7 | 3 | 0 | 2 | 1 | 6 | 14° |
| Totals | 145 | 219 | 158 | 167 | 81 | 75 | 83 | 6 | 2 | 104 | 26 | 33 |

* This was the only occasion upon which a Bristol recording was made for an entire experiment. The experiment was conducted on August 11, and was the sixth in the series of 12. Time scores were computed from the recorded data by counting for each sheep the number of 10-second periods during which the animal had its head in the box for two seconds or longer. This method of scoring, while less accurate than the very laborious procedure of counting actual time in seconds, does not introduce a serious bias, in the opinion of the experimenter.

† The total time of two and one-half hours was divided into nine periods of 16.6 minutes each.

° Maximum score for a single period.

TABLE IV.

Incidence of Coordinate-feeding Between Rams During Experiment Lasting Two and One-half Hours.*

| Pairings | Frequency of coord-feeding | Highest frequency possible† | Coord-feeding ratio |
|---|---|---|---|
| Rams 1 and 2 | 16 | 21 | 16/21 |
| Rams 1 and 3 | 1 | 5 | 1/5 |
| Rams 1 and 4 | 1 | 4 | 1/4 |
| Rams 2 and 3 | 3 | 14 | 3/14 |
| Rams 2 and 4 | 8 | 11 | 8/11 |
| Rams 3 and 4 | 4 | 25 | 4/25 |

* Coordinate-feeding between two rams is said to occur when both of these rams obtain feeding scores of 3 or more during a 100-second period, while the other two rams obtain scores of zero (c.f. first footnote to Table III for unit of scoring). The coordinate-feeding data were obtained from the Bristol recordings and synchronized field notes of the feed box experiment on August 11.

† The highest frequency possible is the total number of 100-second periods during which a given ram could have engaged in coordinate-feeding with the dominant ram by virtue of the fact that the dominant ram was (a) the only other ram at the box, or (b) accompanied at the box by a ram subordinate to the ram in question.

ent Ewes 1 and 2 dominated other animals at the box. Food sharing was common among Ewes 1, 2 and 3. The lambs almost never had exclusive possession of the box, and when at the box they showed no overt aggression.[5] The amount of time that they fed depended on the tolerance of the lambs by the ewes. Hence, differences in the ability of individual lambs to feed are related to differences in ewe-lamb relationships. Field observations furnished ample evidence of the following mother-young relationships: Ewe 3 and Lamb 2, Ewe 1 and Lamb 3, and Ewe 2 and Lamb 4.[6] The yearling was not associated with a ewe in any observable way, either at the box or in the field.

There is reason to believe that the very high feeding score of Lamb 2 was due to an especially close and permissive relationship with its mother. Lamb 2 usually stood very close to its own ewe at the box, and fed whenever she did. Ewe 3 never butted her lamb, although she did not tolerate other lambs. Lambs 3 and 4, on the other hand, did not stay close to their ewes, and often were not at the box when their ewes were feeding. It will be seen in Table III that the feeding scores of Ewe 3 and Lamb 2 are very similar from period to period. The average difference in scores for the same period is only 2.8. Analysis of the Bristol recordings reveals that, of a total of 20 100-second periods during which Ewe 3 fed, her lamb also fed during 17 periods. In contrast with this, Ewe 1 and Ewe 2 fed about as frequently as Ewe 3, but Ewe 1 shared with her lamb only twice, and Ewe 2 never shared with hers.

The lack of agreement between the dominance status of ewes and their lambs may have been noted. Dominance order among the first-season lambs shows no relation to dominance order among the mothers. Of course the number of sheep is much too small to warrant generalizing, but there are two possible correlates of dominance order among first-season lambs that might be mentioned. First, it is possible that dominance among these lambs is related to order of birth, so that lambs born in February tend to be dominant over those born in March or later. There is no way of checking this hypothesis in the present study, since the birth dates of individuals are not known. Stewart and Scott (14) have found that age is favorable to dominance in a herd of goats.

A second hypothesis is that the amount of social distance between a ewe and her lamb will have a direct bearing on the dominance status of the lamb. In the case of Ewe 3 and Lamb 2 extreme social closeness is associated with dominance of this lamb over two other lambs born in the same season. On the other hand, the relationship between Ewe 2 and Lamb 4 (the lamb of lowest dominance status) was the weakest of the three mother-young relationships. Ewe 2 was the least willing to share food with her lamb or to be sucked. Further credence is given to this suggestion by Scott's (11) observations of two orphan lambs which were placed with a flock of domestic sheep. He noted that, "Both orphans appeared to show less fighting than the other sheep . . . and the ram was not aggressive toward other males even in the breeding season." The hypothesis could be tested in a large herd by testing dominance interactions among the ewes and among the lambs over a period of time beginning shortly after the birth of the lambs, and making frequent observations of each ewe with her lamb in isolation from the other sheep.

## LEADERSHIP

Recent studies indicate that leadership may be a behavioral characteristic quite unrelated to dominance status maintained by fighting. The reports of Darling (5) on red deer, Mills (10) and Davis (6) on Rocky Mountain bighorn sheep, and Scott (11) on domestic sheep, all mention that the usual leader in a herd is an old female. Lack of correlation between leadership and dominance interactions has been noted by Allee et al (1) in a flock of ducks, and Stewart and Scott (14) in a herd of goats.

In the present study, clear instances of

[5] The lambs often shoved each other, but never threatened or butted when at the box.

[6] Sucking and following were the principal behavioral indications of mother-young relationships during July, August, and September.

leadership occurred only when the sheep were in a conflict situation involving both a source of attraction and a source of danger in close proximity to each other. The source of attraction was the feed box; danger usually was represented by the presence of a strange person, such as the experimenter. The experimenter discovered that if he stood a few yards behind the box after filling it, the sheep would flock into the center of the field and not advance to feed for several minutes. Finally, Ewe 1 slowly moved forward about ten yards and then halted. Her lamb immediately ran to her. Then the other ewes and lambs, and finally the rams, moved up to her advanced position. If the experimenter withdrew further from the box the process of advancing and halting under the leadership of Ewe 1 might be repeated several times, until the herd finally reached the box. The pattern of advance might vary from day to day, but Ewe 1 always led the others. Sometimes she advanced 15 or 20 yards in front of the herd before they followed her. Sometimes the entire herd moved in single file, with Ewe 1 in the lead and the rams bringing up the rear. The rams rarely came up to the box until Ewe 1 had begun to eat.

Leadership was observed 15 times, always in connection with the feed box experiments. Once the rams dashed ahead of Ewe 1 when she was about five yards from the box, and on two occasions Ewe 2 took the lead after Ewe 1 had led most of the way. But at all other times Ewe 1 moved in advance of the others. There is ample evidence that the sheep were following Ewe 1, rather than just moving toward the feed box. Seven times Ewe 1 did not take the most direct path to the box, but turned and walked at right angles to it for several yards. When she did this, the other sheep continued to follow her just as as though she were approaching the box. When no person was in the field, the sheep moved toward the box more or less independently of each other, but the rams still tended to stay behind the ewes.

On general grounds it would be expected that boldness and leadership were related. In the present study there were no opportunities for observing differences in boldness among the ewes. However, the rams did appear to be more timid than the ewes. A lone ram rarely stayed at the box for more than a few seconds. In all likelihood, when he raised his head from the box and saw that the others had left he would quickly run to where they were. On the other hand, a single ewe might continue feeding alone indefinitely. When the zebra, which had been placed in an adjacent enclosure, suddenly galloped toward the fence, the rams were the first to run from the box and the last to return. This was also true when the experimenter intentionally frightened the herd. The zebra frightened the sheep away from the box about eight times, and each time Ewe 1 led them back. Thus there is considerable evidence that the role of Ewe 1 as leader was not due merely to a greater familiarity with humans.

In the field studies cited above, leadership usually was an important factor in the normal moving about of the sheep and deer. But among the Barbary sheep, instances of leadership were quite rare outside of the special conflict situations described. In wandering and grazing the herd often was scattered widely over most of the field. The rams, ewes and lambs often formed into separate and dispersed sub-groups, yet no consistent leadership was apparent in any one of the subgroupings. What little leading and following there was occurred between lambs and ewes, and between rams and ewes with the onset of sexual activity.

*Ewes and lambs.* During approximately 80 hours of observation from mid-July to mid-September, each first-season lamb attempted to suck its ewe about 20 or 30 times. The usual duration of sucking was only a few seconds, and often the attempt consisted of a single, brief thrust at the udder. Generally the ewe was passive while the attempt was made. Lamb 4, however, often was rejected by its ewe, even though it tried to suck less often than the others. For a while, in fact, its maternal origin was not clear. The lamb alternated between following Ewe 2 and Ewe 4, and twice tried to suck from Ewe 4. Repeated observations confirmed its relationship with Ewe 2. Sucking was accompanied by a certain amount of following of ewes by their lambs. When the herd rested a lamb often lay beside its ewe. The yearling associated wth the other lambs and joined in the general movements of the herd, but did not favor a particular ewe.

*Rams and ewes.* As the rams began to manifest sexual interest in the ewes they gradually spent more time in the company of the ewes and tended to follow them closely during early morning and evening. Before August 15 relatively little following occurred. Perhaps the following of the ewes by the rams in the conflict situations is, in part, the result of conditioning which develops during the rutting season.

## Fighting.

The Barbary sheep would seem to fall about half way between the domestic sheep and the bighorn with regard to amount of fighting. Scott (11) mentioned pushing and shoving among domestic sheep competing for food in winter, and some butting between rams following the same ewe in heat. In contrast, Mills (10) stated that fights between big-horn rams in rut might result in "bleeding noses, splintered horn tips, limping, and skull fractures." No complete comparison can be made with the bighorn because the Barbary sheep were not observed during the height of rutting. There were no observable injuries, and it is probable that the fighting witnessed was far less serious than that associated with breeding.

Two main types of fighting occurred

among the Barbary sheep. One type consisted of a series of head-on charges, usually between rams. The sheep walked away 10 or 15 yards, turned, and walked rapidly toward each other, gradually picking up speed and breaking into a run shortly before they collided. Just before impact their heads were lowered and turned slightly to opposite sides. They attempted to meet squarely with their noses crossed. At the beginning of the charge, the sheep got in step and then tried to keep in step until they struck. If one got out of step they broke off the charge and walked away to charge again. Spencer (13) described bouts between bighorn rams which were very similar in detail. He termed such fights "playful" because one ram would not attack if the other was off balance or not prepared. A fight of this type between Ram 1 and Ram 2 continued intermittently for 25 minutes on August 25. Before that time fights had never lasted more than five minutes.

The second type of fighting consisted of close butting, and locking and twisting of horns. Usually the sheep stood head to head, facing in the same or in opposite directions, and engaged their horn tips. Each tried to twist the head of the other by pulling downward and away. Also, attempts were made to hook the belly or the flank. Fighting of this sort might continue for several minutes. It sometimes started at the feed box as a kind of maneuvering for position.

Until mid-August fighting was almost as common among the ewes as among the rams. The usual fight between ewes consisted of a brief exchange of butts, perhaps with locking of horns and twisting. Charges were very rare. Ewes did not fight with rams.

From mid-August until the termination of the study fighting among the rams increased in frequency, duration and vigor, and was connected with sexual excitement. Rams 2 and 4 were the first to show increased pugnacity and sexual behavior. These rams fought with each other and with the other two rams. Sometimes the penis of a fighting ram emerged briefly from its sheath. By September 10 all four rams had reached a high level of sexual arousal and aggressiveness. Most of the fighting took place in the early morning and in the evening, with relatively little aggressive interaction at the feed box or during the matching tests. Even when Ram 4 was beginning rut and displayed strong aggression toward Rams 2 and 3, he remained rather submissive at the feed box. During the final two days at the box, Ram 4 started fights with Rams 2 and 3. He fought with each male about three times, the average duration of fighting being about two or three minutes. But only once, in a contest with Ram 2, did it appear that he had achieved temporary dominance over his opponent.[7] And only once did Ram 4 achieve dominance in a paired matching test. His opponent in this test was Ram 2. Possibly in the two experimental situations Ram 4 was inhibited by previous experiences of defeat and subordination. Seward (12) with rats, and Ginsburg and Allee (7) with mice, have shown that an animal could be conditioned to defeat much more readily than to victory. Although they did not study the factor of physical environment, it seems reasonable to expect that aggression would be most strongly inhibited in the place where subordination had been experienced most frequently.

Play fighting was frequent among the lambs. Often in the evening they scrambled about, pushing and butting each other, in order to gain a position on top of the rocky hillock in the center of the field. This activity was similar to the children's game, "king-of-the-hill," and has been reported by Darling (5) as occurring among red deer fawns. Sometimes fighting in lambs had a more serious appearance. Two lambs might butt head-on forcefully and in rapid succession until both seemed quite exhausted. There was one instance of a lamb fighting with an adult. Late in August Ewe 4 butted Lamb 3 and the lamb immediately butted back. A short fight ensued, ending with the lamb's retreating and then attacking Lamb 4.

### Sexual Behavior of the Rams.

The first witnessed attempt to mount a female was by Ram 2 on August 10. The ram reared on his hind legs and his penis emerged about three inches from its sheath for a few seconds. The ewe ran off. The ram then tried to mount another ram. Toward the end of August attempted mountings by rams of both rams and ewes were common. This behavior was not observed to occur in the ewes or lambs. Female urine had an excitatory effect upon the rams. The ram sniffed the urines, then curled the upper lip, extended the neck, and tilted the nose in the air. This pattern, according to Spencer (13) is found in bighorns, as well as in other ungulates. Rams sometimes lay on their backs and sucked their penises for short periods. Ejaculation of semen was not observed to occur. Often in the evening, sexual activity and fighting occupied the rams continuously until dark. At no time during observation was a ewe receptive. A ram did not persist in attempting to mount the same ewe. Two tries were usually enough to discourage him. There was no chasing about the field. A ewe had only to walk or run a few yards to get rid of a ram.

### Displaced Aggression.

One of the most striking behavior patterns observed in the course of this study was that in which a sheep responded to a butt, threat or attack from a dominant sheep by delivering in kind to the nearest subordinate. Such "displaced aggression" might continue chain-wise through three or four

[7] The butts exchanged have not been included in the data because the experimenter was engaged in taking motion pictures, and so could not take notes.

individuals, each successive one being lower in dominance. Thus a ram might butt a subordinate ram away from a piece of bread, the latter might butt a ewe nearby, and the ewe in turn a lamb. At the feed box Ram 2 often responded to a sharp butt from Ram 1 by circling the box and butting all the sheep in his path. The examples of displaced aggression are too numerous to be listed. The pattern appeared in rams, ewes and lambs with great frequency. There seemed to be only two factors determining which sheep was to receive a displaced attack, physical proximity and lower dominance status. No special relationships between individuals were apparent, other than the usual ones of dominance-subordination. Winslow (15) found displaced aggression in cats made to compete for food.

## Summary and Conclusions.

1. This study represents an attempt to analyze social behavior and group organization in a small herd of Barbary sheep.

2. Observations and experiments were made on the herd of four rams, four ewes, and four lambs at the New York Zoological Park during the summer of 1947, under conditions with a minimum of human care and interference.

3. In two types of tests it was found that stable relationships of dominance-subordination existed between all individuals, and that the dominance order of all eight sheep was one of straight descent through rams, ewes and lambs.

4. When grain was placed in a small feed box it was found that individual differences in total feeding time at the box were not related to the dominance order. These individual variations probably were due to different rates of food intake and differences in nutritional needs.

5. In the feed box experiments it was found that there was an order of time-of-maximum-feeding which was very similar to the order of dominance.

6. Differences were found in the "social distance" between any two rams when at the feed box. These differences were reflected in the amount of food sharing that occurred and in amount and reciprocity of aggression. Food sharing and aggressive interaction were positively related, and both appeared to be manifestations of the dominant animal's tolerance, or willingness-for-contact with regard to the subordinate.

7. There were individual differences in amount of food sharing and amount of sucking among three ewe-lamb pairs. The dominance status of the lamb seemed to be associated with the social distance between the lamb and its mother. But there appeared to be no relation between the dominance status of the ewe and the dominance status of her lamb.

8. Consistent leadership appeared only in conflict situations characterized by a locus of attraction and a locus of danger in close proximity to each other. In conflict situations a ewe always led, and with only two exceptions it was always the same ewe. The rams were more timid than the ewes in strange and potentially "dangerous" situations.

9. Fighting occurred between rams, ewes and lambs. With one exception, there were no fights between ewes and rams, or between adults and lambs. Ewes fought less than rams, while among lambs play-fighting often was observed.

10. As sexual activity appeared in the rams, fighting became more frequent and vigorous.

11. Dominance relationships between rams remained stable throughout the study and from the time of the first appearance of sexual interest until the study terminated five weeks later.

12. Sexual activity in the rams consisted of attempted mounting of ewes and rams and sometimes of incomplete masturbation. Ewes were not receptive up to September 14, when the study ended.

13. Instances of displaced aggression were very numerous. The recipient was usually the nearest subordinate animal.

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# 4.

## The Pericopidae (Moths) of Kartabo, British Guiana, and Caripito, Venezuela.[1]

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[This contribution is the result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana and to Venezuela, all under the direction of Dr. William Beebe. The Guiana expeditions were made during the years 1917, 1919, 1920, 1921 and 1924. The expeditions were arranged so that each month of the year is represented in the collections. The Venezuelan expedition, in 1942, during which field work was carried on from February 19 to September 2, was sponsored by grants from the Committee for Inter-American Artistic and Intellectual Relations and from four trustees of the Zoological Society, George C. Clark, Childs Frick, Laurance S. Rockefeller and the late Herbert L. Satterlee, and by invaluable assistance from the Standard Oil Companies of New Jersey and Venezuela.]

A total of eight species of Pericopidae were collected at Kartabo and four at Caripito. One species from British Guiana and two species from Caripito are new locality records for their respective countries. One species common to both British Guiana and Venezuela is represented by a new race in Venezuela.

### *Eucyane bicolora* (Sulzer).

Sulzer, Gesch. Ins., t. 22, f. 6 (Expl. Tab.) (1776) (Noctua).

Three specimens taken at Kartabo, two on October 11 and one on December 2. The species has been reported from the Guianas, South Brazil and Peru.

### *Eucyane temperata* Walker.

Walker, List. Lep. Ins. Brit. Mus., 7, p. 1656 (1856).

One specimen taken at Caripito on July 11. The species has been reported from South Brazil, Guianas and Colombia, so this is a new record for Venezuela.

### *Pericopis catilina catilina* (Cramer), new status.

Cramer, Pap. Exot., 1, t. 79. f. E. F. (1775) (Attacus).

In my opinion *Dysschema brotes* (Druce) *Ann. Mag. Nat. Hist.*, 15 *s.* 6, p. 48 1895 (*Anthomyza*) is only the male form and thus a synonym of *Pericopis catilina catilina*. The males in collections are usually named *brotes* and the females *catilina*. The male specimens match Druce's description better since the males are usually blackish-brown rather than the cinnamon brown typical of the females. Furthermore, the character given in the literature to separate the genus *Dysschema* from *Pericopis* is not valid. This character, the length of the pinnae of the antennae double the width of the shaft, is a male sexual character typical of many of the species of *Pericopis*. I am not synonomizing the genus *Dysschema* since the genotype *tiresias* is not available, but the present generic character does not justify the genus. Thus, on the basis of this character the male specimens of *catilina* are assignable to *Dysschema*, hence *brotes*, and the females to *Pericopis*, hence *catilina*.

One male captured at Kartabo on May 24. Recorded from Brazil, Guianas and Colombia.

### *Pericopis catilina angustilineata*, new sub-species.

| *Specimen* | *Sex* | *Date* | *Length of forewing* | *Type* |
|---|---|---|---|---|
| 42487 | male | March 15 | 35 mm. | Holotype |
| 42488 | female | March 16 | 38 mm. | Allotype |
| 4239 | male | March 11 | 38 mm. | Paratype |
| 42489 | male | April 15 | 35 mm. | Paratype |
| 42490 | male | March 15 | 37 mm. | Paratype |
| 42491 | male | June 5 | 35 mm. | Paratype |
| 42492 | female | April 8 | 38 mm. | Paratype |

Head as in *c. catilina*. In the male the length of the pinnae of the antennae is twice the width of the antennal shaft, while in the female the pinnae are barely as wide as the antennal shaft.

Ground color of both the fore and hind-wings blackish-brown to cinnamon brown with bands of greenish-yellow.

The forewing with two semi-hyaline greenish-yellow bands, one median and the other apical as in *c. catilina* with brown or brownish-black veins crossing the bands. The bands differ from those of *c. catilina* in being much reduced; little more or not more than half the width of the bands of *c. catilina*. If one assumes the nomenclatural type to be ancestral, the reduction of the bands has been caused by the encroachment of the brown or blackish-brown scales on both sides of the bands. This is most easily discerned in the median band. The inner side of the band in *c. catilina* crosses the wing nearer to the

[1] Contribution No. 827, Department of Tropical Research, New York Zoological Society.

point where vein $Cu_2$ forks from the cubital stem than it does in *c. angustilineata*. Similar results are obtained if one measures basally from the point where vein $Cu_1$ forks from the cubital stem. In both *c. catilina* and *c. angustilineata*, but particularly in the latter, the encroachment of the ground color on the yellow bands may be seen. The brown scales on the margins of the bands are duller and lighter than the surrounding ground color. This is variable, being more evident in some specimens than others and occurring indiscriminately along the length of the bands. It is most noticeable and frequent on the median bands. The white spots along the outer margin of the forewing are evident to varying degrees. Their place is taken by the brown or blackish-brown scales making up the background. However, all specimens have a streak of white scales on the outer side of the yellow spot which terminates the apical band in cell $M_3$. The spots in cells $M_1$ and $M_2$ appear to vanish first since they are faintly discernible in only one specimen.

The hindwings of *angustilineata*, as in *catilina*, are yellow hyaline for half the length of the wings from the base with a large yellow spot beyond in cells $M_1$ and $M_2$. *Pericopis c. angustilineata* differs in that this large yellow spot is separated from the basal patch by a distance approximately twice that of *catilina*. The part of the basal facies that extends into the proximal part of cell $Cu_1$ is much smaller in *angustilineata* than in *catilina*. The ground color along the inner margins of the hindwings encroaches more on the yellow basal area in *angustilineata* than in *catilina*.

The specimens were all collected during the day while flying. No specimens of Danaidae or Heliconiinae were captured or seen in the same area, though the general appearance and flight of *angustilineata* is suggestive of various members of either of the above groups. The specimens were captured in an area of about one hundred meters' diameter near the end of an unmaintained road going to an abandoned oil well "No. 1". The locality is approximately ten miles west of Caripito, State of Monagas, eastern Venezuela. The area the specimens came from is parched during the dry season, flooded during the wet and characterized by numerous palms and small to very moderate-sized seasonal trees.

**Pericopis tricolora tricolora** (Sulzer).

Sulzer, Gesch. Ins., t. 22, f. 5 (1776) (Noctua).

Three specimens taken at Kartabo; two females on March 22 and one male on November 24. Recorded from eastern Peru, Amazons and Guiana.

**Dysschema heliconides** (Swainson).

Swainson, Zool. 111. (2), 3, t. 124, f. 2 (1833) (Anthomyza).

One specimen collected at Kartabo in 1920. Recorded from the Amazons, Guianas, Colombia and Peru.

**Hyalurga fenestra** (Linnaeus).

Linnaeus, Syst. Ent. (ed. 10), 1, p. 505, n. 41 (1758) (Phalaena).

One specimen collected at Kartabo which represents a new record since the species has only been reported from Brazil and Peru.

**Hyalurga sixola** Schaus.

Schaus, *Ann. Mag. Nat. Hist.*, (8), 6, p. 206 (1910).

A total of seven specimens was taken at Caripito; the males on March 20 (two specimens), April 5, May 12, and May 16 and the females on April 15 and July 2. Recorded from Venezuela and Colombia.

**Hyalurga mysis** (Erichson).

Erichson in Schoenburgk, Brit. Guiana, 3, p. 606 (1848) (Glaucopis).

A female from Kartabo on May 25. Has only been found in British Guiana.

**Hyalurga modesta** Moschler.

Verh. Zool.-bot. Ges. Wien, 27, p. 663, t. 9, f. 29 (1877).

One female at Kartabo on August 19. Recorded from Guiana and Colombia.

**Hyalurga partita** (Walker).

Walker, List. Lep. Ins. Brit. Mus., Het. 2, p. 335, n. 27 (1854) (Dioptis).

Four female specimens at Kartabo; two with no date and the remaining two specimens on November 21 and December 21. One female at Caripito on March 21. Recorded from Brazil, Guianas, Venezuela and Peru.

# 5.

# Report on a Collection of Phalangids from Rancho Grande, Venezuela.[1]

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(Text-figures 1-4.)

[This is one of a series of papers resulting from the 45th and 46th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945 and 1946 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the freshwater lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

This paper is a report on the phalangids collected during the 45th and 46th Expeditions of the Department of Tropical Research.

The species showed relationships to those of Trinidad (Goodnight and Goodnight, 1947), many of the specimens representing the same species. The Cosmetidae, one of the most typical of neotropical families, is here represented by two species, one of which is new.

Among the Phalangodidae, the Stygnommatinae are represented by the wide-ranging *Zygobunus rufus* (Petrunkevitch). This was formerly known only from Panama. The subfamily Phalangodinae is represented by *Kalina tuberculata* Goodnight and Goodnight known formerly only from Trinidad. The Triacommatinae are represented by one new species, *Vima plana*.

Among the family Gonyleptidae, three species are represented, one of which is new.

The writers wish to express their appreciation to Dr. Beebe and Mr. H. Fleming for making this material available for their study. Types are deposited in the collections of the Department of Tropical Research, New York Zoological Society, New York 60, New York.

## SUBORDER LANIATORES THORELL.

### PHALANGODIDAE Simon.

#### Phalangodinae Roewer.

**Kalina tuberculata** Goodnight and Goodnight.

Reference: *Kalina tuberculata* Goodnight and Goodnight, 1947, p. 1, fig. 4.

Record: Zone 28, Rancho Grande, Venezuela, 1945.

#### Stygnommatinae Roewer.

**Zygobunus rufus** (Petrunkevitch).

References: *Stygnomma rufum* Petrunkevitch, 1925, p. 62.

*Zygobunus barronus* Chamberlin, 1925, p. 245; Roewer, 1928, p. 546.

*Stygnommatiplus rufus* Roewer, 1928, p. 544.

*Zygobunus barronus* Goodnight and Goodnight, 1942, p. 4, figs. 10, 11, 12.

Record: Rancho Grande, Venezuela, March 4, 1945.

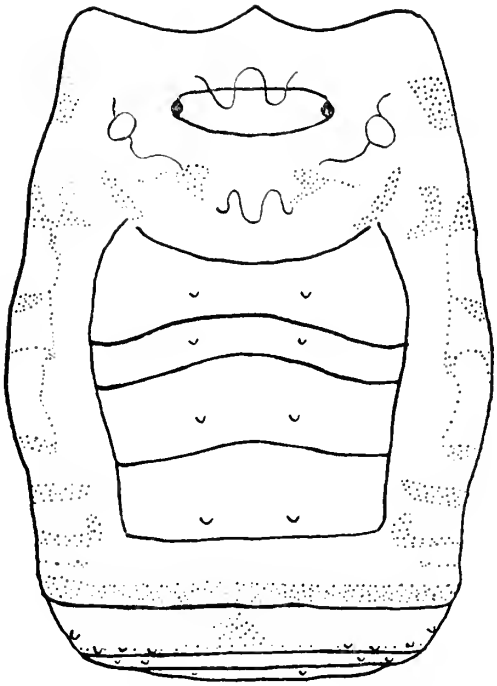
#### Tricommatinae Roewer.

**Vima plana** sp. nov.

(Text-figs. 1 & 2).

Male: Dorsum with five areas, very small paired tubercles on the 1st, 2nd, 3rd and 4th areas. These tubercles are very small and vary in size in different individuals. Cephalothorax smooth, with a low tubercle at the posterior lateral portion. Eye tubercle wider than long, with low tuberculations across the median portion. First area of the abdomen without a median line. Boundaries of areas indistinct, not parallel. Lateral margin of abdominal scute smooth, without median armature. 5th area and free tergites each with a few small granulations. Anal operculum smooth, free sternites each with a transverse

[1] Contribution No. 828, Department of Tropical Research, New York Zoological Society.



TEXT-FIG. 1. *Vima plana* sp. nov. Dorsal view of male holotype.

row of minute tubercles. Spiracle visible. Coxae with a few small granulations; 1st coxa with a transverse row of spines.

First leg slender, unarmed; 2nd to 4th legs heavier, a few scattered tuberculations on the trochanters. Femora with longitudinal rows of spines, remainder of legs only with scattered hairs. 4th patella with a few apical tubercles. Double claws smooth, without scopula or false claw. Tarsal segments: 9-18-8-9. Distitarsus of 1st tarsus with 3 segments, 2nd with 3 also.

LENGTH OF LEGS.

| | I. mm. | II. mm. | III. mm. | IV. mm. |
|---|---|---|---|---|
| Trochanter | 0.3 | 0.7 | 0.8 | 0.8 |
| Femur | 6.3 | 14.4 | 11.5 | 16.2 |
| Patella | 0.7 | 1.2 | 1.4 | 1.5 |
| Tibia | 4.0 | 10.8 | 6.1 | 8.5 |
| Metatarsus | 8.5 | 17.4 | 12.4 | 20.5 |
| Tarsus | 1.5 | 4.5 | 2.9 | 3.2 |
| Total | 21.3 | 49.0 | 35.1 | 50.7 |

Palpus with the trochanter 0.8 mm. long, femur 1.1, patella 0.7, tibia 0.6, and tarsus 0.7. Total length, 3.9 mm. Femur armed retrolaterally as in figure. Prolaterally femur and patella each with a median apical spine. Tibia and tarsus armed as on retrolateral margin.

Proximal segment of chelicera with a dorsal elevation on which are scattered tubercles. Distal segment greatly enlarged.

Body, chelicerae, and palpi light yellowish with scattered black mottlings. First leg uniformly colored; second leg with a white mark at the distal end of the femur; patella black, a white patch at the distal portion of the tibia; third leg with a darker patella but no white markings; fourth leg with a white band following a black band on the distal portion of the tibia. Legs otherwise uniformly dark brown to dusky.

Female: Similar in appearance to male.

Measurements in mm.: Male, total length 3.7; cephalothorax 1.5; width at widest portion 2.6. Female, total length 7.2; cephalothorax 1.7; width at widest portion 4.2.

Record: Male holotype from Rancho Grande, Venezuela, July 22, 1945; paratypes from same locality, March 22, 1945, and July 22, 1945.

Remarks: *Vima plana* is related to *Vima insignis* Hirst. It differs from this latter species by lacking the raised area of the dorsum and the paired low tubercles over the eye.

COSMETIDAE Simon.

Cosmetinae Cambridge.

**Cynorta estebana** Roewer.

Reference: *Cynorta estebana* Roewer, 1947, p. 18, pl. 18, fig. 66.

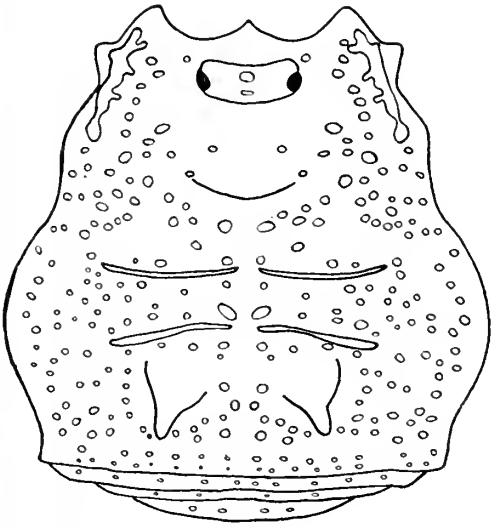
Record: Rancho Grande, Venezuela, August 9, 1945.

**Cynorta bromeliaca** sp. nov.

(Text-fig. 3).

Male: Eye tubercle wider than long. 1st area with a pair of enlarged tubercles, 3rd area with a pair of robust spines which are short and heavy at the base. Remaining areas and free tergites without median armature. Entire dorsum covered with small white elevations. These are more numerous on the lateral posterior portions of the scute. Each free tergite with a transverse row of these same tuberculations. Anal operculum with only a few granulations, free sternites each with a transverse row of hair-tipped granulations. Coxae and genital operculum smooth except for scattered hairs. A few teeth on the anterior margins of the 3rd and 4th coxae, and a transverse row of granulations across the 1st coxa.

TEXT-FIG. 2. *Vima plana* sp. nov. Retrolateral view of palpus of male holotype.



TEXT-FIG. 3. *Cynorta bromeliaca* sp. nov. Dorsal view of male holotype.

Legs clothed only with hairs except for a few tuberculations at the apical portion of the 4th patella; femora straight. Tarsal segments: 6-14-11-12. Distitarsus of both 1st and 2nd tarsi with 3 segments. Proximal portion of 1st tarsus enlarged.

LENGTH OF LEGS.

| | I. mm. | II. mm. | III. mm. | IV. mm. |
|---|---|---|---|---|
| Trochanter | 0.6 | 0.8 | 0.8 | 0.8 |
| Femur | 4.4 | 6.6 | 6.6 | 9.3 |
| Patella | 1.0 | 1.6 | 1.6 | 1.6 |
| Tibia | 2.8 | 8.3 | 3.8 | 5.3 |
| Metatarsus | 4.3 | 10.3 | 5.5 | 9.4 |
| Tarsus | 2.6 | 5.2 | 3.6 | 4.4 |
| Total | 15.7 | 32.8 | 21.9 | 29.8 |

Palpus with the trochanter 0.8 mm. long, femur 1.4, patella 0.9, tibia 1.5, and tarsus 0.8. Total length, 5.4 mm. Palpus characteristically flattened with a ventral row of teeth on the femur.

Proximal segment of chelicera with a dorsal elevation on which are a few granulations. Distal segment somewhat enlarged.

Dorsum reddish-brown, thickly covered with white spots which are more numerous on the lateral and posterior portions of the scute. These form an irregular band of white spots, with a few scattered ones in the median area. Several white spots on the eye tubercle. A transverse row of white spots across each free tergite. Anal operculum without markings. Venter, coxae, and chelicerae reddish-brown with darker markings. Legs yellowish, trochanters, and bases of femora, patellae, and tibiae reddish-brown. Metatarsi white.

Measurements in mm.: Male, total length 6; cephalothorax 1.9; width of body at widest portion 4.1.

Record: Male holotype from bromeliads, Rancho Grande, Venezuela, August 8, 1946.

Remarks: This species is most nearly related to *Cynorta catenulata* Roewer. It differs from this latter species by having an entirely different pattern of white on the dorsal scute.

GONYLEPTIDAE SUNDEVALL.

Cranainae Roewer.

***Poecilocranaus gratiosus*** Roewer.

Reference: *Poecilocranaus gratiosus* Roewer, 1943, p. 54, pl. 7, fig. 63.

Record: Rancho Grande, March 22, 1945.

***Santinezia albilineata*** Roewer.

Reference: *Santinezia albilineata* Roewer, 1932, p. 290, fig. 7.

Record: Rancho Grande, Venezuela, August 1, 1945.

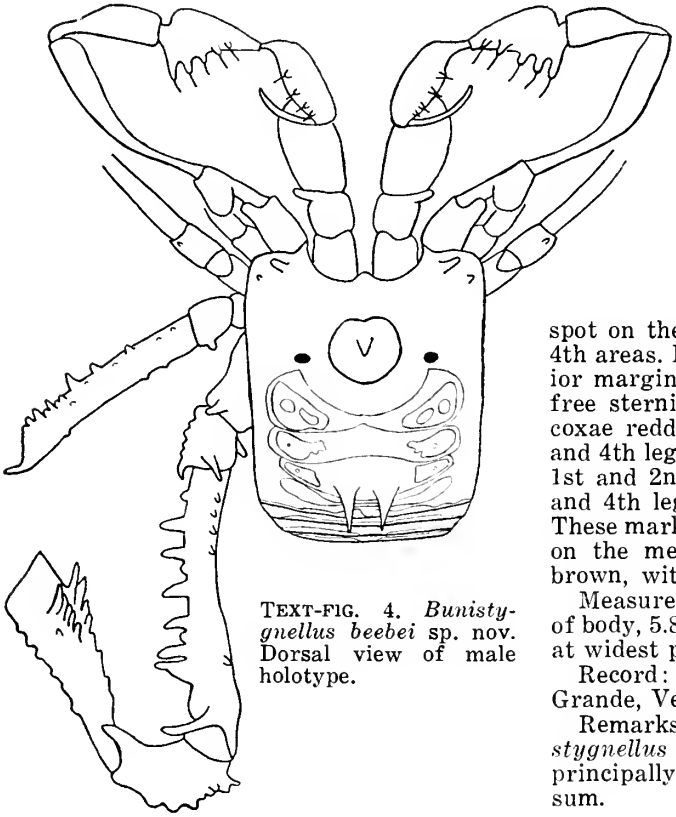
Stenostygninae Roewer.

***Bunistygnellus beebei*** sp. nov.

(Text-fig. 4).

Male: Dorsum smooth, cephalothorax without a median eye tubercle. Eyes widely separated near the posterior portion of the cephalothorax. Between the eyes a large rounded elevation with a short apical spine. Elevation granular. Anterior margin of the cephalothorax with a short anterior projection between the chelicerae and palpi. A large vertical spine at the anterior margin near the coxa of the palpus. A small tubercle at the anterior lateral margin. Abdomen with five areas. 1st area constricted in the middle, 2nd area narrow, 3rd area with a pair of large spines, 4th and 5th areas unarmed. Free tergites smooth, unarmed. Lateral margins of scute smooth, anal operculum smooth. Free sternites each with a transverse row of hair-tipped tubercles which are enlarged into spines at the lateral margin. Spiracles widely open. Coxae covered with hair-tipped tubercles. A transverse row of spines across the 1st coxa. 3rd coxa with anterior and posterior teeth. 4th coxa only slightly projecting and with a large dorsal apical spine.

Trochanters globular. 2nd and 3rd trochanters tuberculate, 2nd with two small dorsal apical spines, 3rd with a posterior apical spine. 4th trochanter very heavy, with a large dorsal apical spine and a lateral spine on each side; covered with smaller tubercles. 1st and 2nd femora clothed only with hairs. 3rd femur covered with hairs and tubercles, ventrally with 2 long rows of spines and with 2 dorsal apical spines. 4th femur tuberculate, ventrally with 2 rows of very large spines, dorsal-apically with 2 large spines. Remaining segments of 1st and 2nd legs clothed only with hairs. Patella of 3rd leg tuberculate with a large ventral apical spine. 3rd tibia with 2 ventral rows of tubercles at the distal third, remainder of 3rd leg unarmed. 4th patella heavily tuberculate and with large apical spines. 4th tibia clavate, with 2 ventral rows of spines at the apical third. Remainder of leg clothed only with hairs. 3rd and 4th tarsi with heavy scopulae, double claws toothed. Tarsal segments: 7-



TEXT-FIG. 4. *Bunistygnellus beebei* sp. nov. Dorsal view of male holotype.

16-8-9. Distitarsi of both 1st and 2nd tarsi with 3 segments.

LENGTH OF LEGS.

| | I. mm. | II. mm. | III. mm. | IV. mm. |
|---|---|---|---|---|
| Trochanter | 0.7 | 0.8 | 1.0 | 1.0 |
| Femur | 3.0 | 4.8 | 3.8 | 4.1 |
| Patella | 0.9 | 1.3 | 1.8 | 2.0 |
| Tibia | 2.0 | 4.3 | 2.6 | 3.3 |
| Metatarsus | 3.2 | 5.0 | 4.0 | 5.0 |
| Tarsus | 1.4 | 4.8 | 2.7 | 3.1 |
| Total | 11.2 | 21.0 | 15.9 | 18.5 |

Palpus with the trochanter 1.2 mm. long, femur 3.6, patella 1.6, tibia 1.9, and tarsus 1.9. Total length, 10.2 mm. Coxa with scattered granulations. Trochanter globular with a dorsal elevation, with a small dorsal and a small ventral spine. Femur curved, unarmed except for a small basal ventral tubercule. No dorsal apical or median apical spine. Patella unarmed, tibia and tarsus each with 5 hair-tipped spines on either side. Tarsal claw long and curved back against the tarsus.

Chelicera greatly enlarged, proximal segment with a dorsal elevation, with several small tubercles dorsal and ventral. A large retrolateral spine at the apical portion. Distal segment huge, elevated considerably over the proximal segment. Distal segment smooth.

Dorsum reddish-brown. Spines and elevation of the cephalothorax likewise reddish-brown. Eyes black. Lateral portions of 1st to 3rd segments with a large white blotch. Within these white areas 1 or 2 circles of reddish-brown. 4th area with a transverse line of white, ending in a wider area at the lateral edge. 4th area with a posterior margin of white. A narrow line of white at the lateral margin of the scute, extending from the anterior portion of the cephalothorax to the 2nd area. A large white spot on the lateral margins of the 3rd and 4th areas. Each free tergite with the posterior margin irregularly lined in white. Last free sternite lined with white. Venter and coxae reddish-brown, basal portions of 3rd and 4th legs likewise reddish-brown. Palpus, 1st and 2nd legs, and distal portion of 3rd and 4th legs yellowish, penciled with gray. These markings give an annulate appearance on the metatarsi. Chelicera dark reddish-brown, with netted dark markings.

Measurements in mm.: Male, total length of body, 5.8; cephalothorax, 3; width of body at widest portion, 4.

Record: Male holotype from Rancho Grande, Venezuela, 1945.

Remarks: This species is related to *Bunistygnellus macrochelis* Roewer, differing principally in the color markings on the dorsum.

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# 6.

## Fresh-water Crabs of the Genus *Pseudothelphusa* from Rancho Grande, Venezuela.[1]

JOCELYN CRANE.
*Research Zoologist, Department of Tropical Research*
*New York Zoological Society.*

(Text-figures 1-3).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest, within a radius of 1 kilometer of Rancho Grande.]

### GENERAL ACCOUNT.

Two species of Potamonidae, both belonging to the genus *Pseudothelphusa,* live within the Rancho Grande area and are common near the laboratory at an altitude of about 3,500 feet. One, *P. garmani,* occurs also farther down, near stream-beds in semi-evergreen seasonal forest, at least to 2,000 feet. The other, the apparently new *P. chacei,* is confined to the cloud forest. Each occurs on both the Caribbean and Valencia sides of the Cordillera.

The general habits are similar in both. Each is occasionally found walking along the damp forest floor, at considerable distances from the small mountain torrents. More rarely the crabs are seen submerged in the streams themselves, clinging tightly to the rocks and moss with their spiny feet. In both species the young are carried principally during the dry season, in March and early April, three females with young having been taken during that season, as well as all of the very small free-living young in the collection. In contrast only one female taken during the rains, in June, carried young. The single female with spermatophores was captured in September; by inference the eggs are laid between October and February, the season during which we have not visited the laboratory.

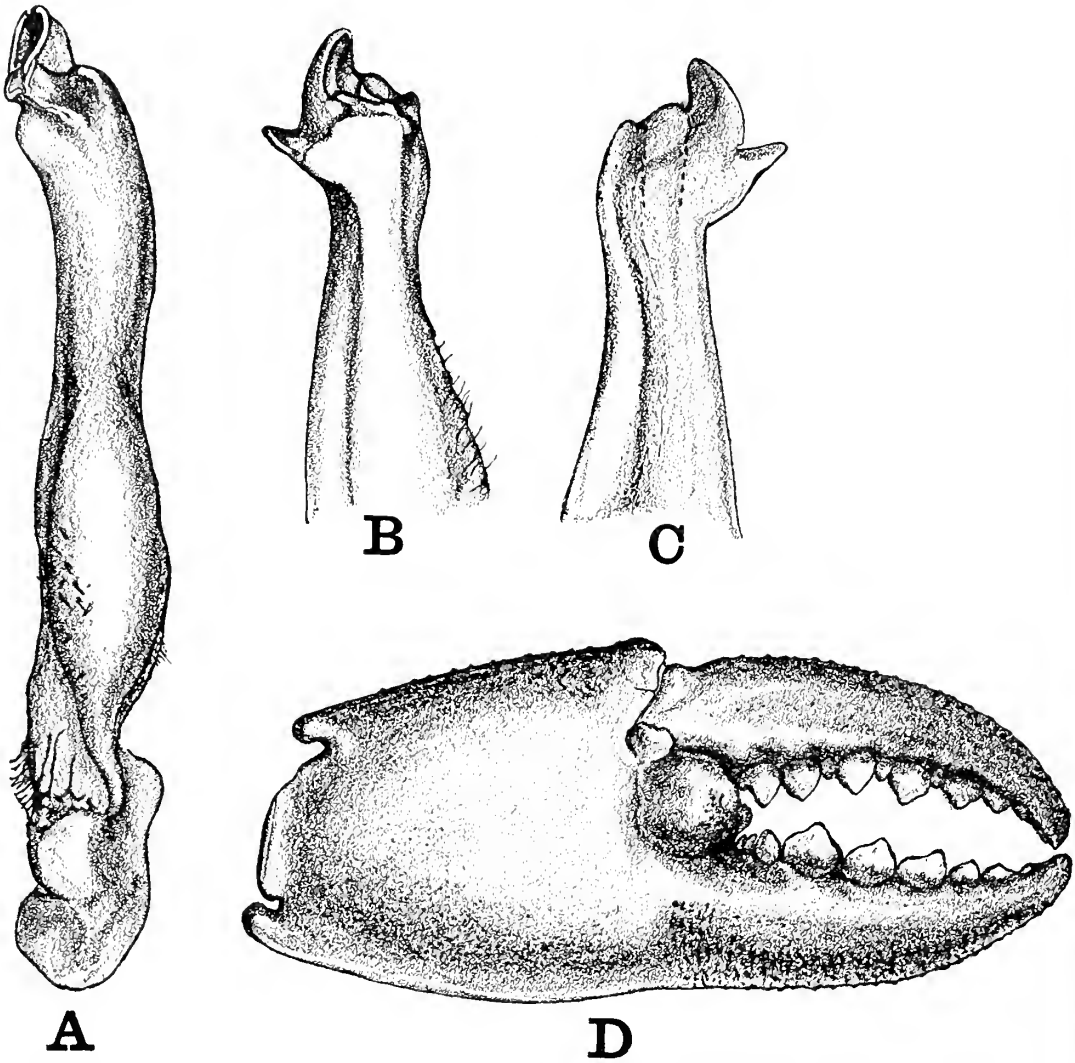
The food of both species consists largely of insects, especially beetles. The remains of eaten crabs are found frequently, and it seems certain that these crustaceans form an important food item in the diet of such local animals as tayras and opossums.

My sincere appreciation goes to Dr. Fenner A. Chace of the United States National Museum for his kindness in determining the identity of *P. garmani* and the systematic status of *P. chacei.* The specimens are in the collections of the Department of Tropical Research of the N. Y. Zoological Society, except for two examples of each species which have been deposited in the United States National Museum. Text-figs. 3A and 3B are the work of Miss Pamela Marmont; the remainder are by Miss Louise Moore.

### Field Key to the Rancho Grande Species of *Pseudothelphusa.*

A. Manus of cheliped with a large tubercle at base of fingers; anterior part of carapace slightly rough to touch; adults large, measuring at least three inches across, females 2¾ inches across still having narrow abdomens; marsupial young numbering between 200 and 300, their front distinctly bilobed and convex; semi-evergreen seasonal and cloud forests ..... *garmani*

[1] Contribution No. 829, Department of Tropical Research, New York Zoological Society.




TEXT-FIG. 1. *Pseudothelphusa garmani.* Adult male, length 47 mm. **A**, right first abdominal appendage, extero-posterior view; **B**, same, extero-anterior view; **C**, same, postero-internal view; **D**, major cheliped, external view.

AA. Manus of cheliped without tubercle at base of fingers; anterior part of carapace smooth to touch; adults small, mature females measuring about 1½ inches across, males less; marsupial young numbering between 20 and 40, their front scarcely lobed, truncate; cloud forest only ..... ....*chacei*, sp. nov.

**Pseudothelphusa garmani** Rathbun, 1898.

(Text-fig. 1, 2A).

*Reference. Pseudothelphusa garmani* Rathbun, 1898, p. 522, text-fig. 14.

*Color in life.* Adults of both sexes: variable shades of dark brown; color of carapace uniformly distributed, the chelipeds, ambulatories and abdomen slightly lighter. Marsupial young: carapace dark brown anteriorly, paler behind; chelipeds apricot buff (Ridgway), deepest on upper merus, carpus and upper half of manus; chelae creamy or white; sides of carapace light brown to buff; sternum and abdomen white; ischium and trochanter of ambulatories buff, other segments dark brown.

*Development.* Two females carried 258 and 260 young, respectively. An example, illustrated in Text-fig. 2A, measures 3.5 mm. in length, 4.7 in breadth. The general form is closely similar to that of the adult, but the front has each of the two distinct lobes more convex and there is no trace of a tubercle outside the manus at the base of the fingers; manus not swollen. No very small free-living examples of this species were taken, but a young female 29 mm. long has the tubercle distinct.

*Food.* Three large examples all contained comminuted black chitin, showing in one case unmistakable beetle elytra; in addition one stomach held soft animal matter, probably worm tissue.

*Habitat and Range.* Taken at Rancho Grande from semi-evergreen seasonal and cloud forests, between 2,000 and 3,800 feet. Previously known also from near Caracas, Venezuela, and from Trinidad.

*Material.* A total of six specimens, not counting marsupial young, have been preserved. Department of Tropical Research Cat. Nos. 4635, male, length 47 mm.; cloud forest, Mar. 28, 1946; 4626, female, 55 mm., Rancho Grande verandah, June 24, 1946, with 260 marsupial young, No. 4626a; No. 45449, 2 immature females, 29, 42.5 mm., cloud forest, April 1, 1945. U. S. Nat. Mus. Nos. 82379, male, length 38.5, cloud forest, Mar. 18, 1946; 82380, female, with spermatophores, length 42.5, semi-evergreen seasonal forest (2000 feet), Sept. 6, 1946.

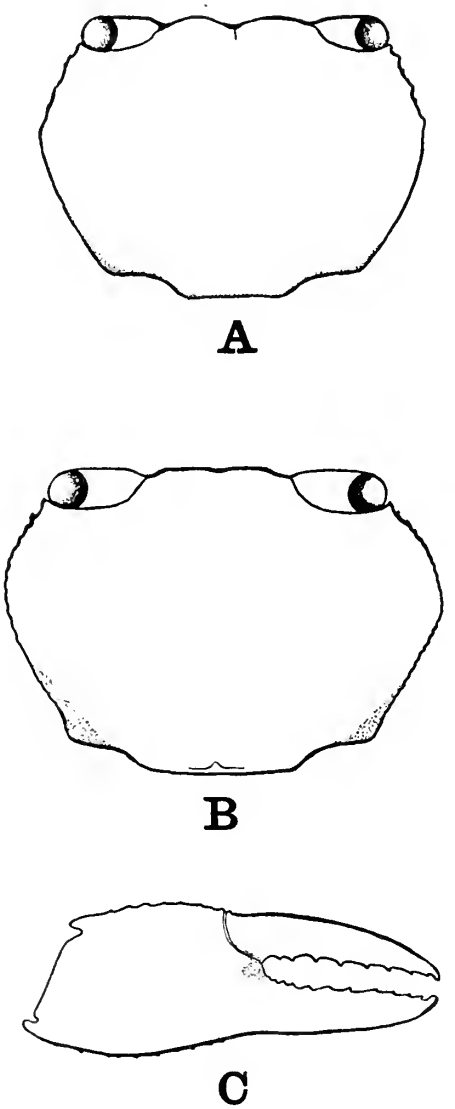
**Pseudothelphusa chacei** sp. nov.

(Text-figs. 2B, 2C, 3).

*Diagnosis*: Superior margin of front distinct and tuberculate but not carinate; bilobed, with median suture present; cervical suture nearly straight; carapace scarcely convex, smooth; exognath of maxillipeds reduced to a stump; manus somewhat swollen; no tubercle at base of fingers; front low; male matures at length of 17 mm., female at about 23.

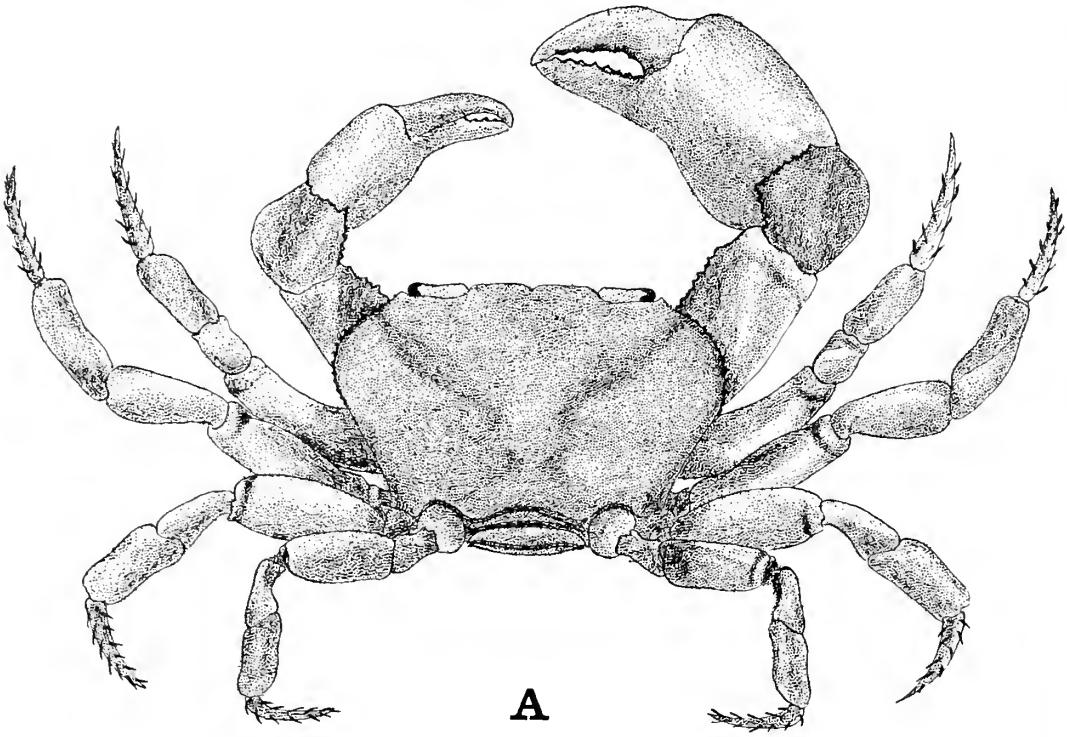
*Description.* Carapace slightly convex, regions scarcely elevated; gastric region slightly less elevated than branchial; anterior margins of protogastric lobes distinct but not prominent; depressions defining anterior part of mesogastric region scarcely indicated; median furrow less well defined than in *garmani*; cervical groove nearly straight, deep, continued practically to lateral margin. Carapace almost completely smooth to the touch, with only a hint of microscopically fine granules in antero-lateral regions. Antero-lateral margins with a small orbital tooth followed by a slight gap; behind this are about 23 to 25 fine teeth, similar and close-set. Front low; superior margin distinct but not carinate, almost truncate, bilobed, finely tuberculate, scarcely or not at all projecting over the vertical surface; in front view slightly depressed in middle; lower margin sinuous, the tubercles tending to be obsolete. Orbits nearly filled by eyes, margins almost smooth, the superior slightly sinuous. Maxillipeds substantially as in *garmani* and *simoni*.

Merus of chelipeds finely rugose above, the inner margin armed with a single line of stout, graduated teeth, the lower and ventrodistal margins by beaded granules. Carpus smooth except for dorso-inner surface which is armed by a crest of small, distinct teeth, of which the usual large tooth is only one exaggerated element. Major and minor manus smooth in both sexes, save for scattered microscopic granules and punctations on outer surface and faint rugosities dorsally. Major manus, especially in male, definitely swollen; upper and lower margins in all slightly convex; sinus at base of pollex practically lacking; no tubercle at base of fingers, although there may be a very slight swelling of the margin at that point; fingers moderately broad, slightly and irregularly punctate, and near dorsal surface of dactyl, tuberculate; prehensile edges practically in contact, the teeth broad, irregular and variable. Merus of all ambulatories flattened, with upper margins convex and finely denticulate; superior margin of carpus and both margins of manus microscopically spinulous; dactyli slender and spined. Male abdominal appendage illustrated (Text-fig. 3).




TEXT-FIG. 2. Young crabs taken from abdominal pouches of female *Pseudothelphusa*. **A**, *P. garmani*, carapace, length 3.5 mm.; **B**, *P. chacei*, carapace, length 3.65 mm. (drawn to same scale as A); **C**, same, right cheliped, outer view, length 2.9 mm.

*Color in Life.* Adults variable and capable to a certain extent of color change, the carapace ranging from a dull red to dark brown. A female with marsupial young had the cara-




TEXT-FIG. 3 [Part]. *Pseudothelphusa chacei* male holotype, length 17.5 mm. **A**, dorsal view; **B**, major cheliped, external view; **C**, right first abdominal appendage, extero-posterior view; **D**, same, extero-anterior view; **E**, same postero-internal view.

pace snuff brown (Ridgway), slightly lighter posteriorly. Chelipeds chiefly cinnamon buff to clay color with snuff brown on dorsal ridge; fingers pale buff; ambulatories snuff brown with darker segment markings. Her young were apricot buff in general coloring; front much darker, almost black; ambulatories cinnamon rufous; dorsal ridges of chelipeds apricot buff; underparts pale buff.

*Measurements.* Holotype male, No. 461197: Length of carapace 17.5 mm.; breadth 28.5; depth 11.5; width of front, lower margin, 7 mm.; major manus (measured along lower margin) plus pollex 26. Paratype female, No. 45105: Length of carapace 23 mm.; breadth 38.5; depth 15; width of front, lower margin, 8.4; major manus (measured along lower margin) plus pollex 30.

*Development.* Two females carried 22 and 40 marsupial young, respectively. An example, illustrated in Text-fig. 2B, measures 3.65 mm. long by 5.0 mm. broad. Compared with the corresponding stage of *P. garmani* the front is scarcely lobed and strongly truncate, the eyes are larger and the cheliped manus is distinctly swollen; the latter difference is carried through into the adult.

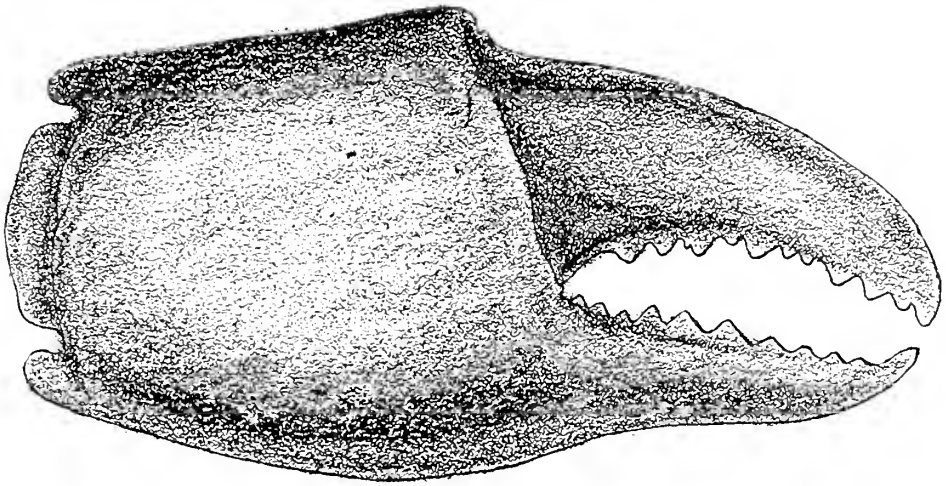
*Behavior of Young.* Samples of the young, when removed from one of the mothers and placed close to her, were almost helpless; they could move feebly, but did not try to climb back into the pouch; one, however, attempted to grip one of her legs as she moved slowly past.

*Food.* A female with young, when captured in an open patio of Rancho Grande, was holding a large, black tenebrionid beetle (D.T.R. No. 45,107) in her major chela, and pulling off the legs with her left. The beetle was uncrushed, being strong and active when liberated. Two of three stomachs examined contained black chitin, including small beetle elytra, in addition to indeterminate soft animal matter; the third was empty.

*Habitat and Range.* Known only from Rancho Grande, in the National Park of Aragua, Venezuela, in the montane cloud forest, between about 3,000 and 3,800 feet.

*Affinities.* Dr. Chace writes as follows regarding this species: "It is very close to Miss Rathbun's *P. simoni.* The male abdominal appendages agree very well with her figure of that species, but your specimens have a somewhat less convex carapace and a sharply carinate upper frontal margin which is completely lacking in *P. simoni.* The general appearance of your material would indicate full specific distinction from *P. simoni*, but the similarity in the male appendages suggests that possibly it deserves only subspecific rank." *P. simoni* is known only from the types, taken from Colonía Tovar and Caracas, Venezuela, and from the "Antilles" (Claudius).

*Material.* A total of 13 specimens was taken, not including marsupial young. The following have been designated as types: Holotype male, Department of Tropical Re-



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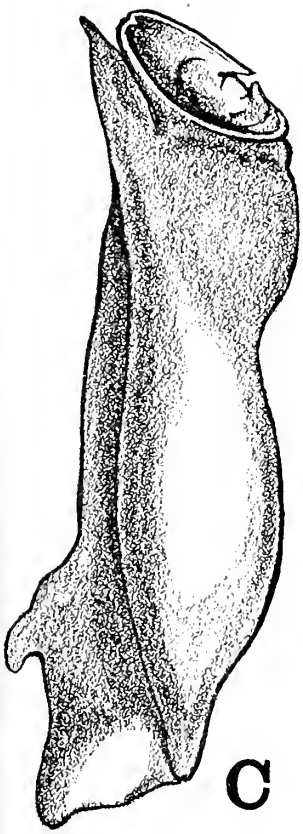

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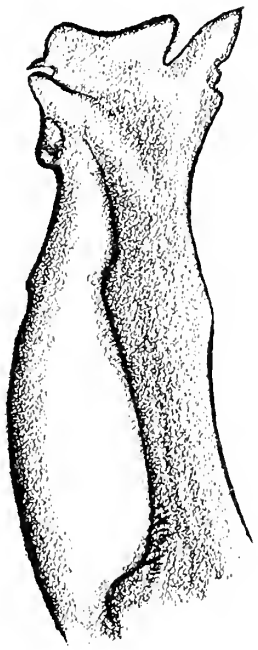

E

TEXT-FIG. 3 [Part]. *Pseudothelphusa chacei* male holotype, length 17.5 mm. **A**, dorsal view; **B**, major cheliped, external view; **C**, right first abdominal appendage, extero-posterior view; **D**, same, extero-anterior view; **E**, same postero-internal view.

search Cat. No. 461197, length 17.5 mm., Rancho Grande court, March 5, 1946; paratype female, D.T.R. No. 45105, 23 mm., with 21 young, Rancho Grande court, March 29, 1945; paratype male, United States National Museum No. 87067, 17 mm., Water Trail, March 15, 1945; paratype female, U.S.N.M. No. 87067, 24 mm., Water Trail, March 7, 1945. In addition, the following were taken, all retained in the collections of the Department of Tropical Research: No. 45106, 1 female, length 22 mm., and 3 young, 7-16 mm., cloud forest, March 20-April 20, 1945; No. 4636, 1 female, length 22 mm., with 40 young, cloud forest, March 14, 1946; No. 461198, 4 young, 7-9 mm., cloud forest, March 1-15, 1946.

It gives me great pleasure to name this species for Dr. Fenner A. Chace, Jr.

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# 7.

# Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela. Part III. Systematics and Behavior in Representative New Species.[1]

JOCELYN CRANE.

*Research Zoologist, Department of Tropical Research, New York Zoological Society.*

(Text-figures 1-8).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water Lake Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

CONTENTS.



[1] Contribution No. 840, Department of Tropical Research, New York Zoological Society.

## INTRODUCTION.

The eight species described in the present paper have been selected from among other Rancho Grande salticids for two reasons. First, they represent a number of different stages and directions in salticid evolution; and, second, special experimental display data and/or examples of the earliest instars have been assembled in each. Part I of this series (Crane, 1948.1) dealt monographically with several species of *Corythalia*, while Part II (1948.2) described the methods of study. In the succeeding parts, which will be based largely on *Corythalia* and the present group of species, it is proposed to discuss the releasing mechanisms of display, to compare post-embryological development and, finally, to evaluate evolutionary trends.

With the exception of Text-figure 8F, which was drawn from life at Rancho Grande by Mr. Kenneth Gosner, all the illustrations are the work of Miss Louise A. Moore.

The types are deposited in the collections of the Department of Tropical Research, New York Zoological Society, New York 60, N. Y.

### *Lyssomanes bradyspilus* sp. nov.

(Text-fig. 1).

*Diagnosis*: Retromargin of fang groove with 6 teeth, the 2 proximal minute, none crowded toward fang base; basal segment of chelicera in male with cluster of 3 to 7 dorsal distal spines; fang toothless; no fringes on first metatarsi, which are straight; no cluster of dorsal tibial spines on palp, its distal apophysis very small, blunt; bulb with three strong, spinous, distal processes; epigynum with two pairs of large rounded bodies distinct, the anterior pair the smaller and practically contiguous. Abdominal black spots present or absent.

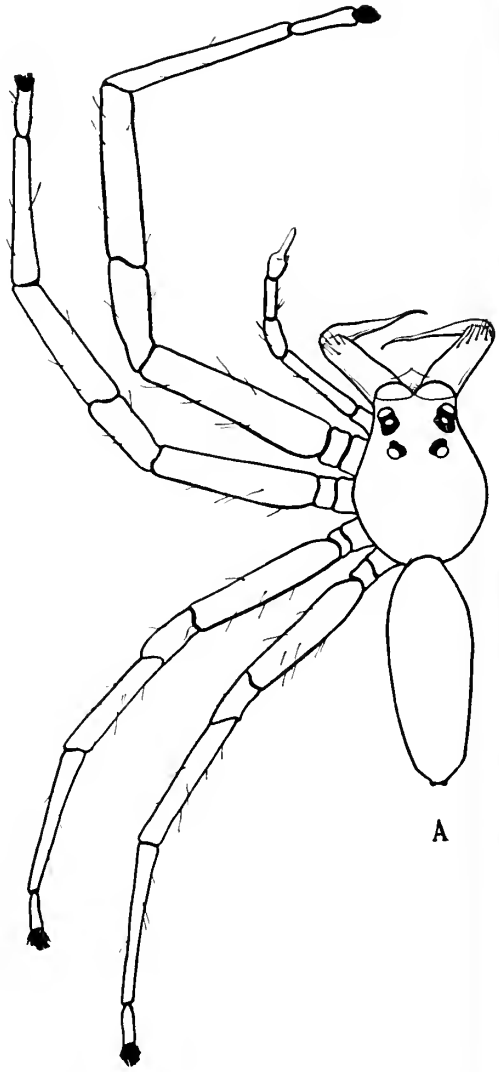
### COLOR.

*Color in Life*: Adult male. Cephalothorax: Integument of carapace translucent green, without dark pigment, varying from a yellowish-green, especially in recently molted

examples, to apple green ( Ridgway). Ocular quadrangle including black eye tubercles with varying amounts and proportions of yellowish- or silvery white and orange-red scale hairs, the latter usually placed anteriorly. AME rimmed with silvery-white; the eyes themselves clear apple green, shifting to black (see under BEHAVIOR) ; other eyes black. A narrow submarginal clypeal band of orange-red scale hairs, directed downward. Chelicerae fangs brown. Palpal bulbs pinkish to orange. Integument of legs translucent apple green, without dark pigment except for black tarsal pads. Abdomen: Integument translucent green, sparsely covered with short hairs, ranging from apple green to dull green-yellow, usually with a short, median basal stripe of darker green. Hairs short, rather sparse, of same color as integument. Paired, subdermal black spots on posterior half of abdomen present or absent, strong or weak, rarely appearing—if at all —until three or four days after final molt; any number up to four pairs may develop. A patch of white hairs often present at distal end of dorsum.

Adult female. Differs from male as follows: Scale hairs of ocular quadrangle, including eye tubercles, tend to be more uniformly yellowish- or silvery white, with the orange-red reduced or absent, except for a variable, sometimes conspicuous, crest behind AME; subdermal clypeal band of orange-red absent, replaced by a band of scant white hairs; palps completely green; legs usually with some dark subdermal pigment concentrated near joints; this often is confined to a single spot in antero-distal part of first tibia. As in the case of the abdominal spots, it develops, if at all, after the final molt. No female seen with more than two pairs of abdominal spots; as in the male, they develop slowly or not at all.

*Color in Alcohol*: All green fades promptly, as usual in the genus, to yellowish-white; no black leg or abdominal pigment remains; on the other hand, the orange-red clypeal band of males and the crest of females are strongly persistent and even intensified.




TEXT-FIG. 1. (Part). *Lyssomanes bradyspilus.* A-D holotype ♂: **A**, dorsal view; **B**, chelicera, ventral view; **C**, left palp, ventral view; **D**, same, ectal view. **E**, paratype ♀: epigynum.

STRUCTURE.

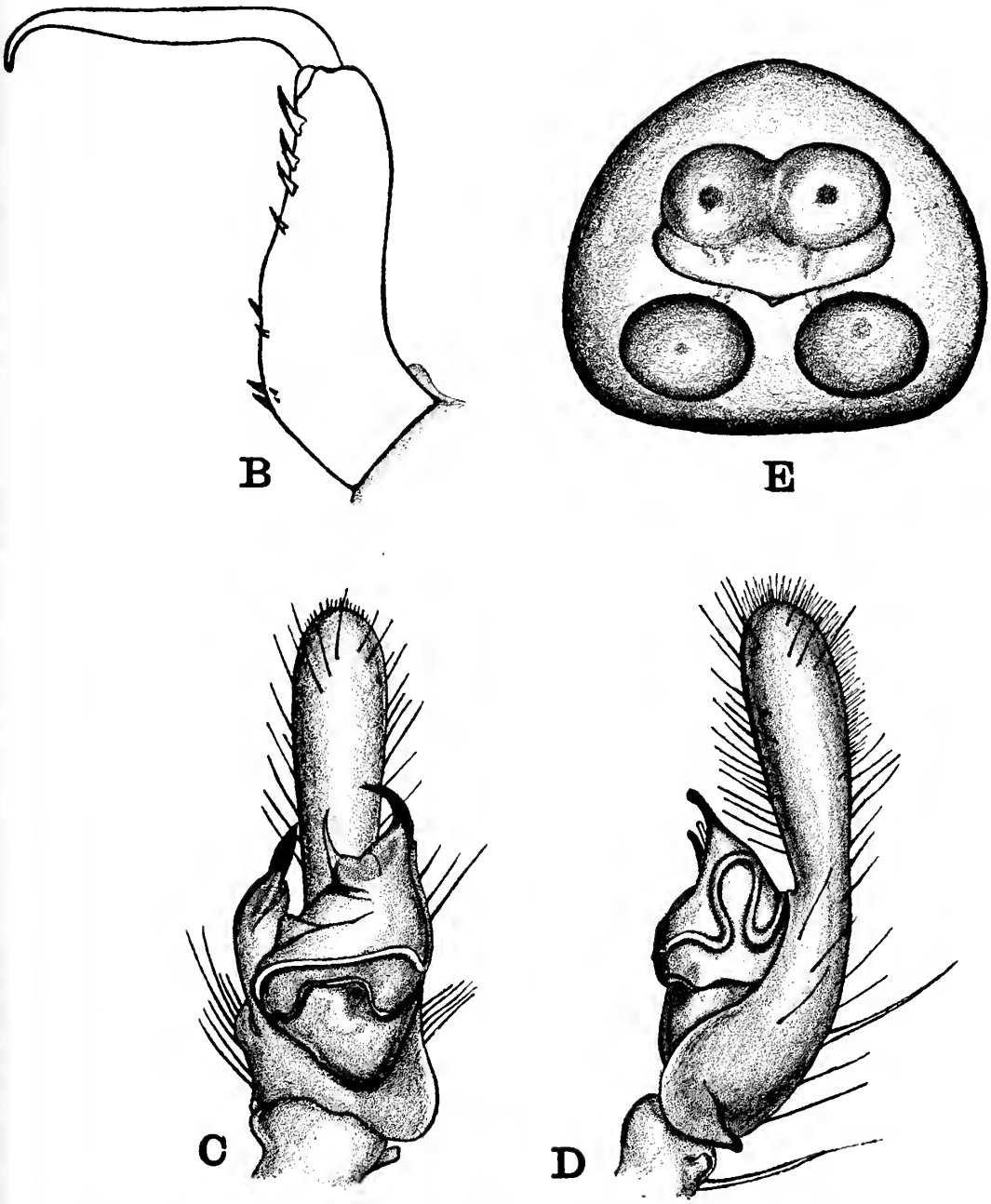
Characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 34.

*Carapace*: Height, including tubercle of PLE, scarcely more than half length; short anterior part of thoracic slope almost level, descent of posterior part moderate; width greatest midway between PLE and pedicel, wider in male (1.5 times height, 79% of length), narrower in female (1.35 times height, 71% of length) ; longitudinal thoracic groove well developed, lying midway between PLE and pedicel.

*Eyes*: Eight eyes in four distinct rows; all except AME elevated on low black tubercles, the PME on same tubercle as ALE. First row 87% as wide as second; length of ocular quadrangle including AME 42% of carapace length, length from ALE to PLE 27%; breadth at ALE much wider than at PLE, 46% and 34% of length respectively; ocular quadrangle length from ALE to PLE only 66% of its breadth at ALE. Diameter of AME 21% of carapace length: ratio of eyes: AME: ALE: PME: PLE: :100: 42: 11. 5: 35. AME practically contiguous, separated from ALE by about a tenth of their diameter; PME slightly closer to ALE than to PLE.

*Clypeus*: Height in males 38% of AME diameter; 54% in females.

*Chelicerae*: In males, strongly produced but of variable length, porrect, robust, divergent. Length of basal segment in best developed more than half carapace length, in least developed about half. Each with 1-2 prs. of overlapping spines near base on medial front




TEXT-FIG. 1. (Part). *Lyssomanes bradyspilus*. A-D, holotype ♂: **A**, dorsal view; **B**, chelicera, ventral view; **C**, left palp, ventral view; **D**, same, ectal view. **E**, paratype ♀: epigynum.

margin, and a group of 3 to 7 strong distal spines, the number and arrangement varying even on two sides of same individual. Fang slender and sinuous, toothless; groove weak; promargin with three small teeth near base, the smallest proximal, it and the next closer together than second and third; no tooth at base of fang; inferior margin typically with 6 teeth in a straight row, increasing in size distally, along entire edge of groove. The basal one or two, however, although apparently constant, are minute, delicate and easily destroyed; they are separated considerably from each other and the distal 4, which are quite evenly spaced. In females the chelicerae are, of course, much shorter; distal spine group absent; teeth closer together, tending to be evenly spaced throughout and of more nearly equal size.

*Maxillae*: Parallel; width 60% of length; distal dilation slight; external angle evenly rounded without tubercle.

*Lip*: Breadth 90% of length; basal excavation extending 25% of length; distal end reaching slightly beyond middle of maxillae; sternal suture straight.

*Sternum*: Broadly scutiform; width 85% of length in males, slightly less in females; equally wide between second and third coxae; base of lip 60% as wide as anterior border in males, 50% in females; posterior end a bluntly rounded lobe extending about halfway between fourth coxae, which are separated by two-thirds of their diameter.

*Legs*: Tibial indices: Holotype male, first leg 12, fourth leg 11; paratype female, first and fourth legs, 13. First legs of male considerably elongated and enlarged. See Table I for formula.

TABLE I.

*Lyssomanes bradyspilus*: Leg Formula.

| | 1 | 2 | 4 | 3 |
|---|---|---|---|---|
| Male holotype | 3.8 | 3.0 | 3.0 | 2.9 |
| | 1 | 4 | 2 | 3 |
| Female paratype | 3.2 | 2.9 | 2.7 | 2.6 |

All legs with little hair; hairs on metatarsi arranged clearly in dorsal and ventral rows, but in no sense profusely enough to be called fringes.

*Spines*: (Male holotype and female paratype). First and second legs: Femur dorsal 1-1-1; prolateral and retrolateral 0-1-1. Patella 0 but with a long, slender dorsal distal bristle. Tibia: Prolateral 1-1; retrolateral 1-1 in male, and on second female leg, 0-1 on first female leg; ventral 2-0-2-2, not opposite, the distal ones not terminal. Metatarsus ventral only 2-2-2, not terminal. Third leg: Femur as in first and second. Patella dorsal distal only 1. Tibia, dorsal 1-0-0-1; pro- and retrolateral, as in first and second male; ventral 0-0-2-0. Metatarsus, prolateral and retrolateral 1-1-0; ventral, male, 2-0-0, female none. Fourth leg: Femur dorsal 1-1-1; pro- and retrolateral male 0-0-1, female none. Patella as in third. Tibia dorsal as in third; pro- and retrolateral as in first and second male, except fourth female prolateral is 0-1; ventral none. Metatarsus ventral only 1 (retro) -0-0. In addition, there are rudiments on third and fourth legs of distal metatarsal spines, 2 prolaterals, 2 retrolaterals and 2 ventrals, all minute and very weak. Palpal spines: Femur dorsal 0-1-1; pro- and retrolateral distal 1; patella, dorsal distal 1; tibia, prolateral male, 0-1, female, 1-1; metatarsus female, dorsal 1-0; pro and retrolateral 1-1.

*Abdomen*: About 3 times longer than broad in males and young females, tapering from level of genital groove; anal tubercle not pronounced; vestigial colulus not indicated.

*Palp*: Femur slightly curved; patella and tibia nearly equal; tibia without dorsal spine cluster; tibial apophysis scarcely more than a truncate tubercle opposing basal ridge of tarsus; bulb with three pointed distal processes, variously shaped, and a distal tubercle (see Text-fig. 1), the whole complex structure differing only in proportions and details from Chickering's description of the palp in *L. banksi* (1946, p. 12).

*Epigynum*: No median notch. Two pairs of large, rounded bodies; members of anterior pair smaller, apparently contiguous; posterior pair separated by less than half their own diameter.

MEASUREMENTS.

Male holotype. Total length in alcohol 4.7. mm.; carapace length 2.1; carapace breadth 1.6; carapace height 1.1; ocular quadrangle length, AME to PLE .89, ALE to PLE .58; ocular quandrangle breadth, at ALE .96, at PLE .72; diameter AME .45, ALE .19, MLE .05, PLE .15; clypeus height .17; basal segment chelicera 1.1; patella breadth, 1st leg .38, 4th .24.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1st | 2.3 | .96 | 2.1 | 2.0 | .55 | 7.9 |
| 2nd | 1.9 | .75 | 1.6 | 1.7 | .41 | 6.4 |
| 3rd | 1.8 | .68 | 1.4 | 1.7 | .41 | 6.0 |
| 4th | 1.7 | .65 | 1.5 | 1.9 | .44 | 6.2 |
| Palp | 1.0 | .44 | .41 | — | .58 | 2.4 |

Female paratype. Total length in alcohol 4.7 mm.; carapace length 2.1; carapace breadth 1.5; carapace height 1.1; ocular quadrangle length, AME to PLE .89, ALE to PLE .65; ocular quadrangle breadth, at ALE .99, at PLE .72; diameter AME .45, ALE .19, AME .05, PLE .15; clypeus height .24; basal segment chelicera .75; patella breadth 1st leg .34, 4th .24.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1st | 2.0 | .79 | 1.8 | 1.7 | .41 | 6.7 |
| 2nd | 1.7 | .75 | 1.4 | 1.5 | .38 | 5.7 |
| 3rd | 1.6 | .68 | 1.2 | 1.5 | .38 | 5.4 |
| 4th | 1.9 | .55 | 1.4 | 1.8 | .41 | 6.1 |
| Palp | .82 | .44 | .44 | — | .68 | 2.4 |

BEHAVIOR.

*Locomotion*: This species is a typical runner; I have never seen it jump, except in a final short pounce upon prey. The spider runs in brief spurts, during which the palps hang down practically touching the ground; during the pause they palpate the surface. No special use is made of the first legs, which take an active part in running.

*Courtship Display*: In Stage I, the carapace is held high, the first three pairs of legs braced somewhat forward, obliquely, and the fourth pair back; the palps hang over chelicerae, now and then tapping ground, while the abdomen hangs straight down. To superficial observation, the display consists only of posing in this position, varied with occasional bobbing of the carapace and twitching of the abdomen during rising excitement. Not until Stage II is reached, within touching distance of the female, are the first legs raised; they are then extended to the front, while the carapace sinks low and the abdomen is swung back in the horizontal position.

When the spiders are observed from their own level, however, in a straight front view, it is obvious that during display the rate of

activity of the muscles controlling the antero-median eyes is considerably increased; this gives rise to a much accelerated color "change" of the eyes, from green to black to green again. Similar eye color shifts have been known for many years in a few other salticids (e.g. Bristowe 1941, p. 419 ff. and references). It is apparently caused by slight motions of the long, cone-shaped optic "cups," possibly concerned with a change in focus, or in the lateral range of vision, although the exact mechanism does not seem to have been worked out. In *Lyssomanes* the shifts take place slowly but continuously during ordinary daily activity, and may be observed at close range under a binocular microscope. The mechanism works independently in the two eyes, and at a given instant either or both eyes show any proportion of green or black. To human beings, at least, the asymmetrically rolling effect is startling. In a dorsal view, the slight motions of the elongate "cups" may be simultaneously viewed through the translucent cuticle of the carapace.

Bristowe suggests the possibility that the color shifts may be useful in enticing prey. However that may be, after the Rancho Grande observations it seems to me highly probable that acceleration of muscular activity during display should be considered as a definite part of the behavior pattern, probably with an adaptive significance; its relative value among the various sign stimuli has not yet been established. This entire subject will be further considered in subsequent papers.

Once her attention has been attracted, the female usually sits quietly, sagging to one side on several folded legs; during the male's display, the rate of her ocular muscular activity also is increased.

*Threat Display*: Males usually took no notice of one another, and were induced to display only three times. During these periods, eye color shift was not especially noted. No differences were observed between threat position and activity from those of courtship, except that the carapace and abdomen were neither bobbed nor twitched. I never saw the long chelicerae unsheathed, although twice there was a brief, butting skirmish before one opponent retreated.

*Habitat*: Known only from the cloud forest near Rancho Grande. Shaken from green herbs, shrubs and low trees; one example taken from an epiphytic bromeliad growing twenty feet from the ground.

*Affinities*: This species holds its chief characteristics in common with a number of *Lyssomanes*, although their combination seems quite distinct. *L. quadrinotatus* Simon, (1900), from nearby mountains, has only three teeth on inferior margin of fang groove.

*Material*: A total of 7 adult males and 4 females have been preserved in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 461199, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1136 meters; cloud forest; March 20, 1946.

PARATYPE: Female. Cat. No. 45450, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 9, 1945.

The name *bradyspilus* is proposed in reference to the delayed development of the black markings after the final molt.

### **Semorina brachychelyne** sp. nov.

(Text-fig. 2).

*Diagnosis*: Small, brown, scale-less salticids, carapace low, abdomen long and narrow with a very slight constriction near middle, first legs greatly elongated and enlarged, extended forward and scarcely used in walking, while the abdomen is frequently elevated. Chelicerae in male scarcely a fourth length of carapace; tibial apophyses of palp both curved.

#### Color.

*Color in Life*: Adult male. Carapace integument dark brown, without scales and almost without hairs, except around eyes. AME clear ochraceous brown shifting to black. Palps dark. First legs brown, the femur and tibia almost black, the tarsi and sometimes the metatarsi translucent horn-color. Other legs translucent horn. Abdomen covered with fine dark brown hairs with a pair of small spots of white hairs (not scales and not shiny or iridescent) three-fifths of distance from base to tip. In one male there was a pair of faint pale spots near tip of abdomen in addition to the distinct more anterior pair.

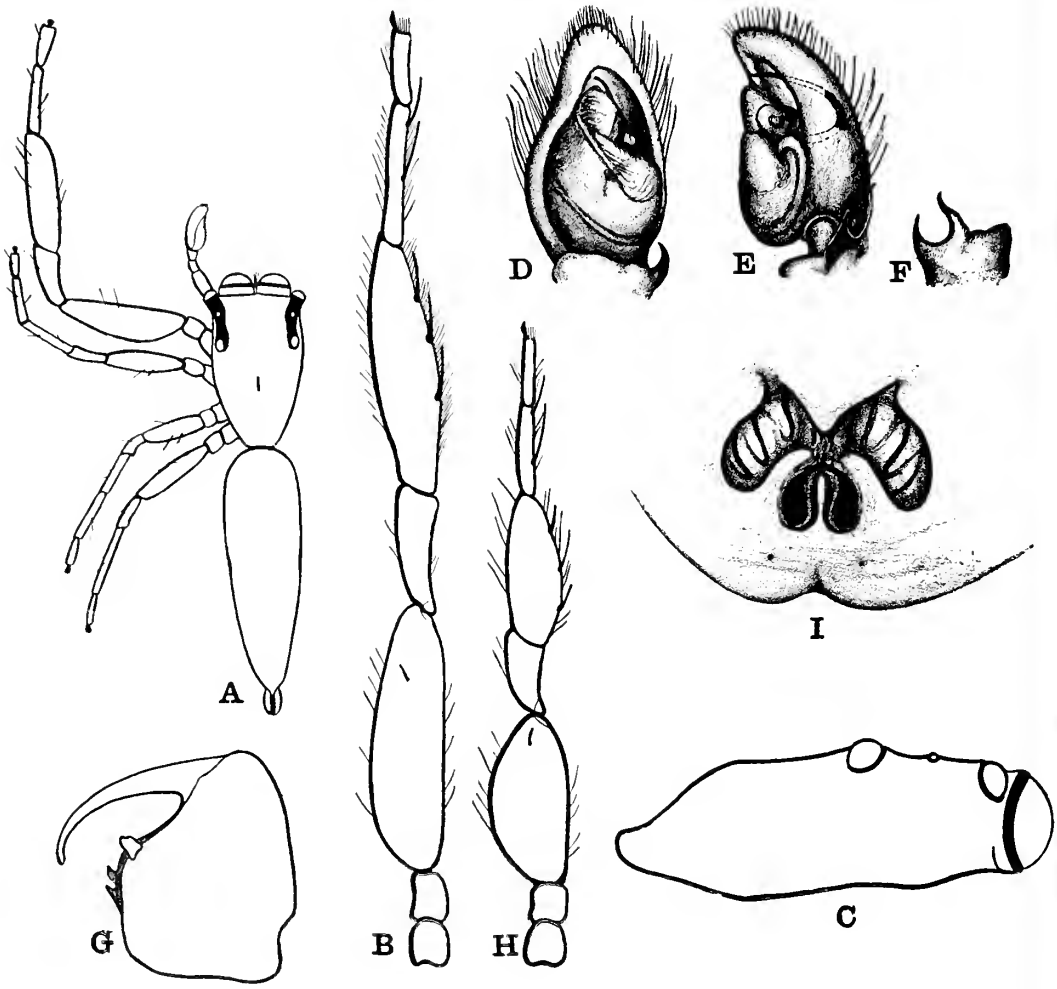
Adult female. Carapace integument yellowish-brown except sternum which is faintly pinkish. Eyes surrounded by a few yellowish hairs. Eyes themselves as in male. Tibia and tarsus of palps shiny silvery white, very conspicuous when vibrated. Swollen tibia of first legs with a ventral dark spot extending laterally; entire first leg darker than the others, which are pale translucent yellow-brown. Abdomen with a median, slightly darker stripe giving off three pairs of dark cross bars reaching middle of side. A median dark spot immediately before tip of abdomen.

*Color in Alcohol*: The white spot(s) of the male abdomen are practically invisible, the pattern now resembling closely that of the female, which is little altered from life.

#### Structure.

The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 37.

*Carapace*: Height only 30% of carapace length; postocular plateau long; thoracic




TEXT-FIG. 2. *Semorina brachychelyne*. A-G, holotype ♂: **A**, dorsal view; **B**, first leg, anterior view; **C**, carapace, lateral view; **D**, palp, ventral view; **E**, same, ectal view; **F**, same, tibial apophysis; **G**, chelicera, ventral view. H-I, paratype ♀: **H**, first leg, anterior view; drawn to same scale as B; **I**, epigynum.

slope slightly concave; width of carapace greatest at level of PLE, about twice height, and 60% of carapace length. Longitudinal groove well defined, in middle of postocular plateau.

*Eyes*: Eyes occupying slightly less than one-half length of carapace. Ocular quadrangle only a third as long as broad, the sides practically parallel but with PLE very slightly closer together than ALE. Carapace extending moderately beyond PLE at their level; PME median, or slightly nearer ALE than PLE. Diameter of AME about 21% of carapace length; ratio of eyes, holotype: AME : ALE : PME : PLE : : 100 : 41 : 7 : 3 : 41. AME practically contiguous, separated from ALE, which are recurved, by about one-third diameter of ALE.

*Clypeus*: Height in male only 5 to 6% of AME diameter, in female 11 to 12%.

*Chelicerae*: Short, divergent, 25% of carapace length in male, slightly shorter in female. Two small teeth on superior, one larger on inferior margin.

*Maxillae*: Length 54% of width in male, 64% in female; outer distal margin a blunted, obtuse angle, not produced.

*Lip*: Width 55% of length in male, 78% in female. Sternal suture straight.

*Sternum*: Width 56% of length in males, 53% in females. Anterior margin straight, a little narrower than lip base, greatest width between posterior margins of first legs; posterior end tapering, blunt-tipped extending between fourth coxae; the latter separated by less than a quarter of their thickness.

*Legs*: Tibial indices: Holotype male, first leg 17, fourth leg 14; paratype female, first leg 23, fourth leg 12. First leg in both sexes much elongated and enlarged with the femur and tibia especially deep (tibia depth of first leg in male 30% of its length, in female 45%). See Table II for formula. Hair scanty

except as follows. In male, first tibia and metatarsus with a short, moderately dense ventral fringe of dark hairs, and a scantier dorsal one of pale hairs; second tibia with a very scant pale fringe, dorsally and ventrally, metatarsus with a similar, slightly longer one ventrally only; third and fourth legs with very scanty ventral metatarsal fringes only. Fringes of negligible development in female.

TABLE II.

| | 1 | 4 | 2 | 3 |
|---|---|---|---|---|
| Male holotype | 2.5 | 1.8 | 1.6 | 1.3 |
| | 1 | 4 | 2 | 3 |
| Female paratype | 1.6 | 1.6 | 1.3 | 1.1 |

*Spines*: (From male holotype and female paratype). Femur, dorsal 0-1-1-1 throughout, the proximal two weak, bristle-like, especially in female. Patella spineless throughout. Spines otherwise as follows: First leg: Tibia, ventral only 0-2-2-2, the latter not terminal; metatarsus, ventral only 0-2-2. Second leg: Tibia, retro-ventral only 1-1-0; metatarsus, male 0, female 0-2. Third leg: Tibia and metatarsus 0. Fourth leg: Femur, retrolateral distal in male 1, in female 0; tibia and metatarsus 0.

*Abdomen*: Very elongate and tapering in both sexes, the breadth about a third of length, a very slight constriction near middle.

*Palp*: Femur practically straight; tibia more than one-half length of patella; two lateral tibial apophyses, the more dorsal longer, tapering, recurved at tip, the more ventral shorter, strongly curved antero-inwardly. Embolus slender and tapering. Distal part of bulb with a conspicuous, chitinized, knob-like protuberance directed outward.

*Epigynum*: An anterior pair of kidney-shaped bodies, diverging posteriorly; a posterior pair, smaller and closer together, followed by a pair of conspicuous small dark spots; a broad and shallow marginal notch.

### Measurements.

Male holotype. Total length in alcohol 5.3 mm.; carapace length 2.2, breadth 1.3, height .68; ocular quadrangle length .79, breadth 1.2; diameter AME .46, ALE .19, PME .03, PLE .19; clypeus height .02; basal segment of chelicera .55; sternum length .86, breadth .48; patella breadth, 1st leg, .38, 4th .21; abdomen length 3.2, breadth .99.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.7 | .89 | 1.5 | .96 | .48 | 5.5 |
| 2 | 1.1 | .51 | .79 | .65 | .31 | 3.4 |
| 3 | .82 | .38 | .58 | .68 | .31 | 2.8 |
| 4 | 1.1 | .51 | 1.0 | .89 | .38 | 3.9 |
| Palp | .72 | .24 | .14 | — | .62 | 1.7 |

Female paratype. Total length in alcohol 5.3 mm.; carapace length 2.2; carapace breadth 1.3; carapace height .65; ocular quadrangle length .79; ocular quadrangle breadth 1.2; diameter AME .45; ALE .19 PME .03, PLE .19; clypeus height .05; basal segment of chelicera .50; sternum length .96, breadth .50; patella breadth, 1st leg, .32, 4th .15; abdomen, length 3.2, breadth 1.1.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.1 | 5.8 | .92 | .65 | .38 | 3.6 |
| 2 | .82 | .48 | .62 | .51 | .44 | 2.9 |
| 3 | .79 | .34 | .44 | .55 | .34 | 2.5 |
| 4 | 1.0 | .48 | .79 | .75 | .48 | 3.5 |
| Palp | .65 | .27 | .24 | — | .44 | 1.6 |

### Behavior.

*Locomotion*: The movements of this spider in the field are absurdly reminiscent of those of scorpions or pseudoscorpions, and bear little resemblance to ant behavior. Their small size, however, makes the existence of an adaptive mimetic function extremely questionable. They are to be counted among the runners in the family, their progress being a rapid sort of scurry, with short jumps reserved for crossing gaps in the terrain, or, of course, for the final stage in catching prey. During running the palps are vibrated continually up and down, while the first legs are held straight out in front, the metatarsi and tarsi curved inward; these legs are often vibrated, scarcely or not at all touching the ground, almost as rapidly as the palps. Meanwhile the abdomen is frequently elevated and waved slightly, also in the vertical plane. Immature specimens show all these characteristics in progress, and they are typical of locomotion whether or not another individual is present. Both abdomen and first legs are invariably raised whenever any obstacle is encountered.

*Courtship Display*: Indistinguishable from ordinary locomotion except that the first legs are extended at a wide angle (more than 90%) and slightly more elevated, the tarsi usually bent down; often the palps are held still; there is the usual pursuit with sidling, and the abdomen, with increasing excitement, tends to remain elevated. Motionless posing with abdomen up and first legs extended at the usual angle, also occurs with excitement. In Stage II the first legs are brought close together in front, about as in simple locomotion. During courtship the female vibrates her white palps rapidly, once her attention has been gained.

*Threat Display*: No threat displays were seen, although a number of attempts were made to induce them.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from shrubs and low trees.

*Affinities*: This species differs from Simon's Venezuelan species, known only from females (*S. seminuda* and *S. iris*, 1901), in the complete lack of shining abdominal scales in any specimens. It likewise appears distinct from Mello-Leitao's *S. lineata* (1945)

from the Argentine. No other species seem to have been referred to this genus. It differs clearly from the other Rancho Grande species (see below) in details of the chelicerae, palp and epigynum.

*Material*: A total of 5 adult males and 4 adult females have been preserved, in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 481558, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1136 meters; cloud forest; July 15, 1948.

PARATYPE: Female. Cat. No. 461200, Department of Tropical Research, New York Zoological Society; Limon Gorge, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1100 meters; lower edge of cloud forest; April 20, 1946.

The name *brachychelyne* is proposed in reference to the relatively short chelicerae.

### **Semorina megachelyne** sp. nov.

(Text-fig. 3).

*Diagnosis*: Very similar to *S. brachychelyne* in general appearance. Chelicerae elongated, about half carapace length in male; tibial apophyses of palp slender and straight.

#### Color.

*Color in Alcohol*: Both sexes scaleless, brown except for pale second, third and fourth legs; no distinct and unvarying spots or other markings.

#### Structure.

Does not differ significantly from *S. brachychelyne* except as follows: Height of carapace slightly more in male (33% of length, instead of 30%); thoracic groove less distinct, transverse rather than longitudinal; ALE and PLE slightly larger, almost one-half diameter of AME. Ratio of eyes, holotype: AME:ALE:PME:PLE::100:48:8:48. Clypeus even narrower, in both sexes, about 4% of AME in male, 5.4% in female. Maxillae and sternum both narrower with little sexual difference in breadth.

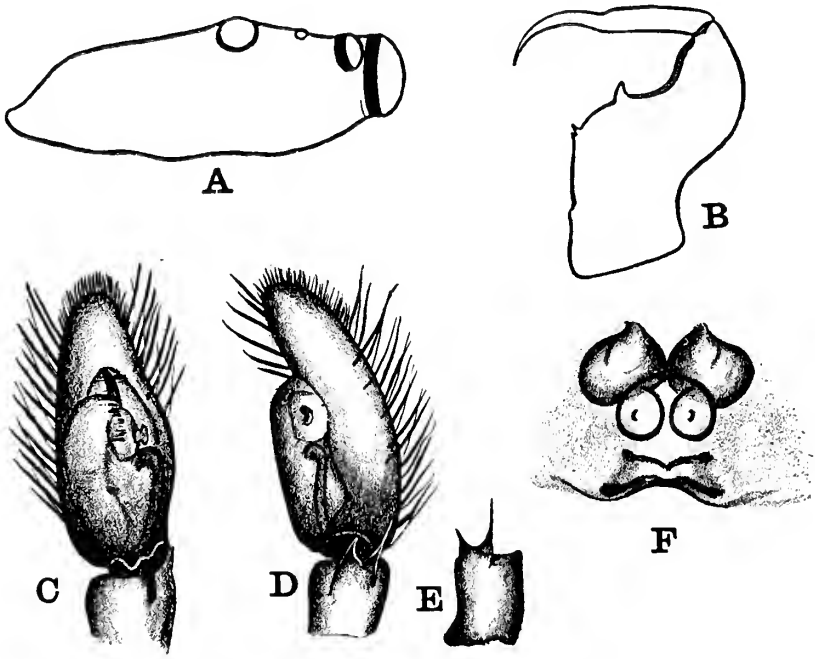
*Chelicerae*: These form a major specific difference, being long in males, the length of the basal segment 50% of carapace length; in females it is only 30%. They are held almost horizontally in both sexes, but are more divergent in males than in females. Tooth on inferior margin relatively larger in males of present species than in *brachychelyne*.

*Legs*: Tibial indices: Holotype male, first leg 12, fourth leg 12; paratype female, first leg 20, fourth leg 15. General form, proportions and fringes similar to those in *brachychelyne*. The leg formula is given in Table III.

TABLE III.

*Semorina megachelyne*: Leg Formula.

| | 1 | 4 | 2 | 3 |
|---|---|---|---|---|
| Male holotype | 2.3 | 1.7 | 1.5 | 1.2 |
| | 1 | 4 | 2 | 3 |
| Female paratype | 1.5 | 1.4 | 1.1 | 1.1 |




TEXT-FIG. 3. *Semorina megachelyne*. A-E, holotype ♂: **A**, carapace, lateral view; **B**, chelicera, ventral view; **C**, palp, ventral view; **D**, same, ectal view; **E**, same, tibial apophysis. **F**, paratype female: epigynum.

*Spines*: (From male holotype and female paratype). As in *brachychelyne*, except for second leg, as follows: In male, metatarsus retroventral 1-0, not 0; female, as in *brachychelyne* male, except metatarsus is 1r-2.

*Palp*: Differs from *brachychelyne* as follows: Both tibial apophyses are straight, the tarsus along with its bulb is more slender, and the coiling of the tubule within the bulb is different.

*Epigynum*: The structure differs distinctly in the two species, as shown in the figure; the more nearly spherical shape of the four bodies is especially noticeable.

MEASUREMENTS.

Male holotype. Total length in alcohol 4.7 mm.; carapace length 2.2, breadth 1.3, height .75; ocular quadrangle length .79, breadth 1.2; diameter AME .43, ALE .21, PME .03, PLE .21; clypeus height .02; basal segment of chelicerae 1.1; sternum length .96, breadth .46; patella breadth, 1st leg .27, 4th .17; abdomen, length 2.5, breadth .82.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.5 | .82 | 1.4 | .96 | .41 | 5.1 |
| 2 | .96 | .51 | .75 | .62 | .34 | 3.2 |
| 3 | .82 | .38 | .55 | .68 | .27 | 2.7 |
| 4 | 1.1 | .48 | .92 | .85 | .38 | 3.7 |
| Palp | .72 | .31 | .17 | — | .58 | 1.8 |

Female paratype. Total length in alcohol 4.0 mm.; carapace length 1.7, breadth 1.0, height .55; ocular quadrangle length .75, breadth .96; diameter AME .36, ALE .16, PME .03, PLE .17; clypeus height .09; chelicera, basal segment .52; sternum length .79, breadth .36; patella breadth 1st leg .21, 4th leg .14; abdomen, length 2.3, breadth .79.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | .79 | .48 | .58 | .44 | .27 | 2.6 |
| 2 | .62 | .34 | .41 | .31 | .24 | 1.9 |
| 3 | .55 | .31 | .34 | .41 | .27 | 1.9 |
| 4 | .79 | .31 | .62 | .55 | .27 | 2.5 |
| Palp | .44 | .17 | .14 | — | .34 | 1.1 |

*Behavior*: Locomotion as in *brachychelyne*. No displays observed.

*Habitat*: Known only from lower edge of montane cloud forest, about 3,500 feet, near Rancho Grande. Collected from tree trunks and shrubs.

*Affinities*: See remarks under *brachychelyne*.

*Material*: A total of 2 adult males and 5 adult females were taken, along with a number of young. The following have been designated as types:

HOLOTYPE: Male Cat. No. 461201, Department of Tropical Research, New York Zoological Society; Water Trail, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1100 meters; lower edge of cloud forest; May 5, 1946.

PARATYPE: Female. Cat. No. 461202. Same data as holotype.

The name *megachelyne* is proposed in reference to the long chelicerae of the male.

### ***Ashtabula furcillata*** sp. nov.

(Text-fig. 4).

*Diagnosis*: Color in life above entirely iridescent green with white dorso-lateral band encircling carapace and abdomen; dorsal abdominal spots lacking, although sometimes faintly indicated in alcohol; carapace low; abdomen elongate; tibial apophysis of male forked.

COLOR.

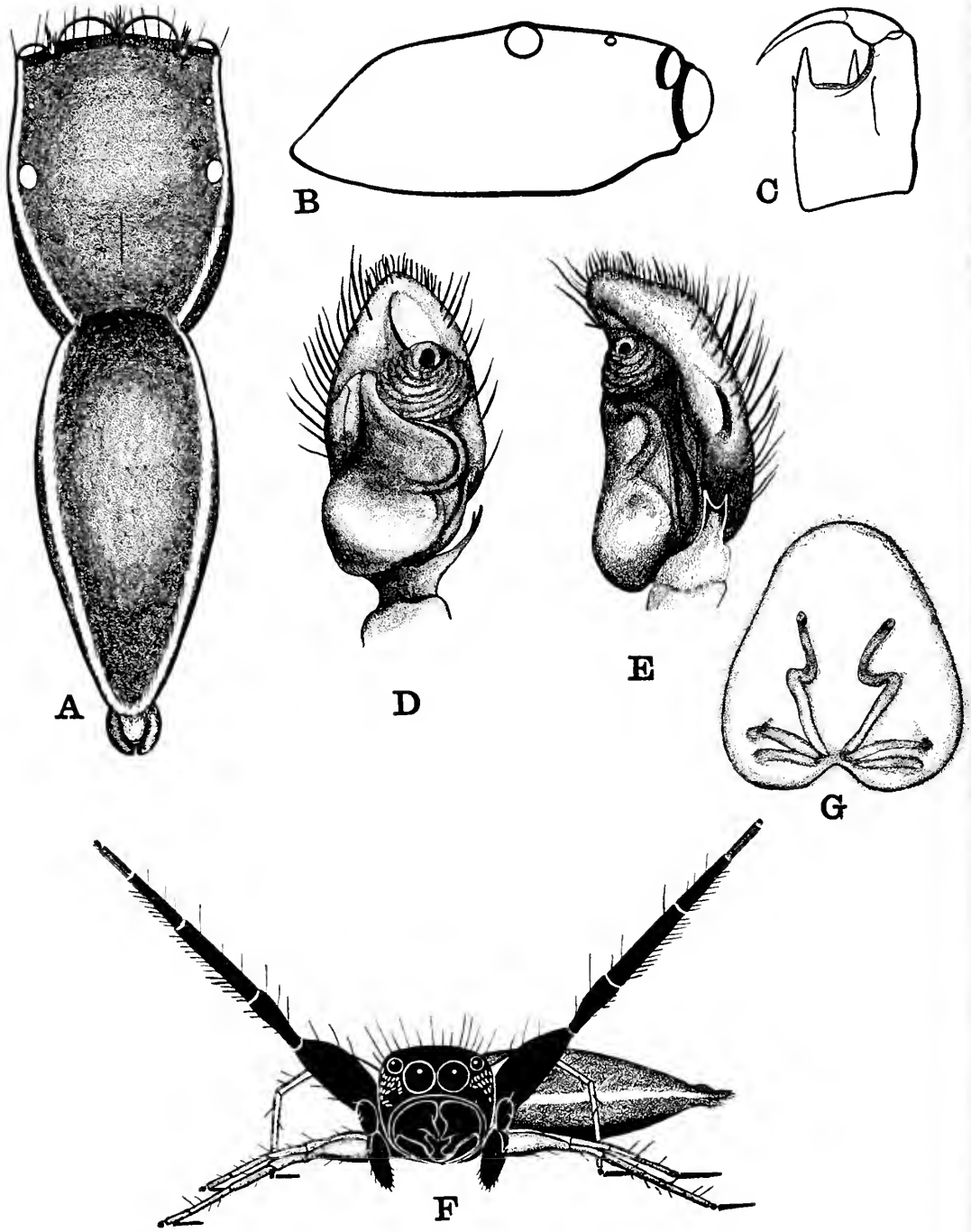
*In Life*: Adult male. Carapace above entirely covered with iridescent scales, rich green with bronze reflections. A white stripe starting behind ALE, bordered narrowly on ventral margin with black, passing immediately below PME and PLE, and extending along thorax almost to pedicel. Sides of carapace naked, black with a narrow white submarginal border of scales. AME narrowly rimmed with yellowish. Clypeus black, naked. Palps and first legs black (except pale 1st tarsi), other legs translucent buff. Sternum black. Abdomen covered with green scales like those of carapace, outlined dorso-laterally with white, which either continues to tip of abdomen or stops short of the tip; a white distal median spot present or absent. Moderate green iridescence on lower abdominal sides, below white stripe; venter black.

Adult female. Like male, except sides of carapace brown, not black; palps light green-yellow, not black; first legs dark brown, not black, the distal metatarsus and entire tarsus paler; other legs pale as in male, but with greenish tinge.

*In Alcohol*: The green iridescence is almost or completely lacking, and the scales may be largely missing, especially on the abdomen, where there may be faint traces of median spots or other markings. The white dorso-lateral bands, however, are very persistent.

STRUCTURE.

Essentially as in Chickering's description of *A. dentata* Cambridge, 1901 (Chickering, 1946, p. 248). The only significant differences are as follows: *Chelicerae*: Large prolateral tooth of basal segment of chelicera straight, not curved; enlargement at base of fang less distinct, a tubercle rather than a tooth. *Fringe* on first leg continues onto metatarsus. *Spines*: Very similar in the two species; the femoral prolateral distal spines tend to be more numerous than in *dentata* (first leg 2, not 1; 4th leg, male, 1 not 0, but 0 in female); metatarsal prolaterals tend to be fewer than in *dentata* (second leg 0, not 1; third leg 1, not 2); a weak fourth metatarsal ventral distal is present in *furcillata*, absent in *dentata*. Female *furcillata* as in male, except that femoral distal spines are reduced, about as in male *dentata*, and tibials are completely absent. *Palp*: Tibial apophysis differs radically from that of all pre-




TEXT-FIG. 4. *Ashtabula furcillata.* A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, chelicera, ventral view; **D**, palp, ventral view; **E**, same, ectal view; **F**, courtship display. **G**, paratype ♀: epigynum.

viously known males—*zonura* Peckham, 1894, *dentata* Cambridge, 1901, and of *dentichelis, sexgutta* and *glauca*, all of Simon, 1902; in *furcillata* alone it is not simple, but distally forked.

MEASUREMENTS.

Male holotype. Total length in alcohol 4.2 mm.; carapace length 1.9, breadth 1.4, height .75; ocular quadrangle length .82, breadth 1.2; diameter AME .34; ALE .17; PME .04; PLE .17; clypeus height .05; basal segment of chelicera 2.4; patella breadth, 1st leg, .19, 4th .21; length of abdomen 2.3, breadth 1.1.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.2 | .79 | .99 | .79 | .41 | 4.2 |
| 2 | .82 | .44 | .55 | .48 | .31 | 2.6 |
| 3 | .79 | .38 | .51 | .51 | .31 | 2.5 |
| 4 | .99 | .51 | .72 | .58 | .34 | 3.1 |
| Palp | .68 | .14 | .10 | — | .62 | 1.5 |

Female paratype. Total length in alcohol 3.7 mm.; carapace length 1.7; carapace breadth 1.1; carapace height .68; ocular quadrangle .79; ocular quadrangle breadth 1.1; diameter AME .33; ALE .17; PME .04; PLE 17; clypeus height .03; basal segment of chelicera .36; patella breadth, 1st leg .26, 4th .21; length of abdomen 2.0, breadth 1.0.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | .82 | .55 | .62 | .48 | .31 | 2.8 |
| 2 | .68 | .38 | .44 | .38 | .27 | 2.2 |
| 3 | .68 | .38 | .38 | .41 | .31 | 2.2 |
| 4 | .85 | .44 | .65 | .51 | .31 | 2.8 |
| Palp | .44 | .21 | .41 | — | .38 | 1.4 |

Tibial indices: Holotype male, first leg 11, fourth leg 17; paratype female, first leg 22, fourth leg 19. See Table IV for formula.

TABLE IV.

*A. furcillata*: Leg formula.

| | 1 | 4 | 2 | 3 |
|---|---|---|---|---|
| Male holotype | 2.2 | 1.6 | 1.4 | 1.3 |
| | 1 | 4 | 2 | 3 |
| Female paratype | 1.6 | 1.6 | 1.3 | 1.3 |

BEHAVIOR.

*Locomotion*: A scurrying run, the first legs held flat and low, straight in front of body; both they and the palps palpate the surface almost constantly during progress. During pauses the first legs are usually elevated, and they and the palps jerked rapidly up and down. Both *Ashtabula* and *Sassacus* are masters of backward running, and both can jump well, although they never resort to it except in crossing gaps and in the final stage of prey capture.

*Courtship Display*: *Stage I.* Male carapace well elevated, abdomen swung to one side (usually the left), where it is held low, practically resting on ground; the spider sidles back and forth, raising the front legs at a wide angle and waving them up and down in unison. The palps occasionally jerk up and down, but hang quietly during height of display. The white abdominal stripe and its bounding iridescence show clearly, little impeded by the short, pale, posterior legs. When the attention of a female has been gained, her pale, greenish-yellow palps jerk up and down rapidly and almost continuously, being conspicuous against her dark brown clypeus and mouthparts. *Stage II.* Not seen.

*Threat Display*: Inter-male display seems feebly developed in this species; three different pairs of males at various times, all in display condition, judging by their behavior toward females, paid little or no attention to each other, except for some brief elevation of the forelegs, which frequently takes place in any situation and appears to be of an exploratory nature.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always taken on herbs, shrubs and low trees.

*Affinities*: Close to *A. dentata;* see remarks under *Structure*. It seems likely that *dentata, dentichelis* and *furcillata* will prove to be no more than subspecies of *zonata*.

*Material*: A total of 5 adult males and 1 adult female have been preserved. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 461203, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 15, 1946.

PARATYPE: Female. Cat. No. 481559, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 21, 1948.

The name *furcillata* is proposed in reference to the characteristic forked tip of the palp's tibial spine.

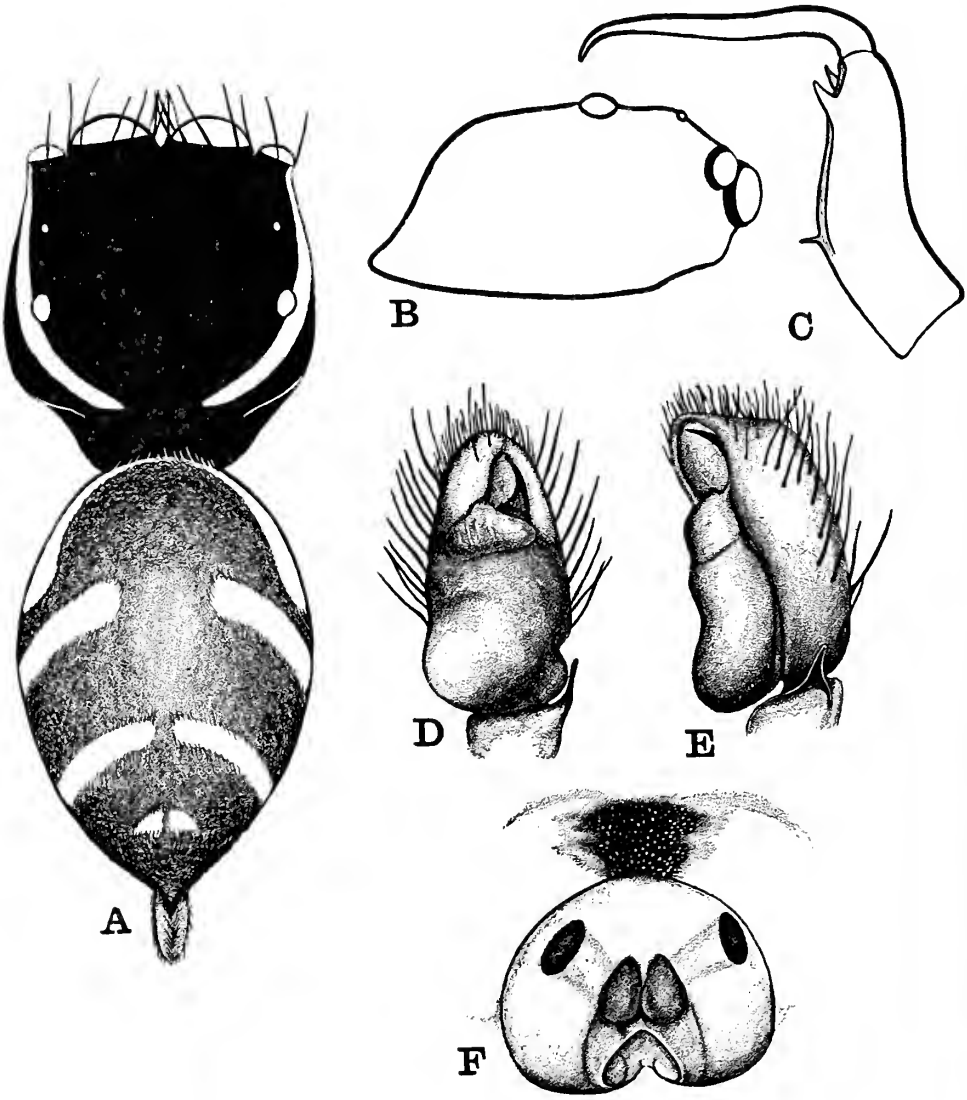
**Sassacus flavicinctus** sp. nov.

(Text-fig. 5).

*Diagnosis*: Male black with yellow on clypeus, in paired stripes and a submarginal band on carapace, and in transverse markings on abdomen. Female brown with obscure ochraceous markings. Chelicera of male strongly produced, the promargin with two teeth, far separated, the retromargin with a single strong tooth near distal end. Tibial apophysis of palp strong, simple, tapering, tip slightly recurved; embolus curved.

COLOR.

*Color in Life*: Adult male. Cephalothorax: Integument of carapace black, with a moderate number of long bristles in ocular region, and with lemon yellow (Ridgway) scales arranged in dense bands as follows: A pair on carapace just below dorsal eyes, converging slightly behind them and ending, without meeting, halfway down thoracic slope; a narrow submarginal band; a well-developed band of scales and scale-hairs




TEXT-FIG. 5. *Sassacus flavicinctus*. A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, chelicera, ventral view; **D**, palp, ventral view; **E**, same, ectal view. **F**, paratype ♀: epigynum.

completely covering and slightly pendent from the narrow clypeus. Mouthparts and legs black except as noted below; all tarsi brown; tibia and metatarsi of all except first legs banded brown and black in varying proportions; all legs with small anterior patches of yellow and white hairs and scales on some or all of the following segments: Femur, patella and tibia; these markings are highly variable. Sternum black with white hairs, which occur also on underside of coxae. Abdomen: A basal semi-circular band of lemon yellow scales continuing backward a third of abdominal length; behind this two pairs of short, curved bars, concave posteriorly, of which the posterior pair may join in the midline; at tip of abdomen a tiny round spot, or a short bar concave posteriorly, may be present or absent. Center black with a triangular patch of white hair, the apex posterior.

Adult Female. Cephalothorax: Carapace black with rather weak markings of ochraceous brown scale-hairs as follows: Across clypeus and completely encircling sides of carapace and thoracic slope, absent only in middle of ocular quadrangle. Palps dark with yellowish hairs. Legs banded light and dark brown. Sternum black.

Abdomen: Dorsum with an indistinct, interrupted reticulated pattern which consists basically of an anterior basal band, followed by several pairs of hollow bands; the latter do not meet in midline, but join with the preceding band by a narrow stripe just before the center; tip of abdomen covered with

ochraceous hairs. Venter black with a few scattered light hairs.

All scale-hairs easily removed, and frequently absent in preserved specimens.

### Structure.

The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given below.

*Carapace*: Height about half (female) or slightly less than half (male) of carapace length; anterior part of thorax flat, with a very gentle slope, rounding into rounded sides of cephalic part; descent of posterior part (less than half postocular length) abrupt, slightly concave; width of carapace greatest a little behind PLE, 1.5 times height, 67% (male) to 75% (female) of carapace length; thoracic groove scarcely indicated.

*Eyes*: Length of ocular quadrangle about 58% as long as broad, its sides almost parallel, though very slightly wider at ALE than at PLE; carapace extending slightly beyond PLE at their level, PME slightly nearer ALE than PLE. Diameter of AME about 20% of carapace length; ratio of eyes, holotype: AME: ALE: PME:PLE::100:48:8:44. AME practically contiguous, separated from ALE, which are slightly recurved, by about an eighth of their diameter.

*Clypeus*: Height 12% of AME diameter.

*Chelicerae*: In males strongly produced, held almost parallel to ground, divergent; length of basal segment about three-fifths of carapace length. Promargin with one slender tooth at proximal end of groove and one, long, robust, triangular, far removed, near base of fang; slightly proximal to this on retromargin a single large tooth. Fang slender, slightly sinuous. Chelicerae of females much shorter with a very short groove flanked on promargin by two teeth close together, the proximal the smaller, and one large tooth on retromargin.

*Maxillae*: Width about 75% of length; outer distal edge in male more dilated and obtusely angled than in female.

*Lip*: Breadth more than 90% of length; distal end reaching slightly beyond middle of maxillae; sternal suture curved, especially in male.

*Sternum*: Width 62% of length in males; wider, about 73%, in females. Anterior margin concave, narrower than base of lip; greatest width between first and second legs; posterior end bluntly pointed, extending slightly between fourth coxae; the latter separated by less than half their diameter.

TABLE V.

*S. flavicinctus*: Leg Formula.

| | 1 | 4 | 2 | 3 |
|---|---|---|---|---|
| Male holotype | 1.8 | 1.5 | 1.4 | 1.35 |
| | 2 | 1 | 3 | 4 |
| Female paratype | 1.8 | 1.65 | 1.7 | 1.4 |

*Legs*: Tibial indices: Holotype male, first leg 16, fourth leg 17.5; paratype female, first leg 26, fourth leg 23. First femur in both sexes enlarged, and entire first leg somewhat thickened and elongated in male. See Table V for formula. All legs with little hair.

*Spines*: (From male holotype and female paratype). Patella without spines throughout. First leg: Femur, dorsal 3 in distal half; prolateral distal 1 in male, 2 in female; tibia ventral only 1r-2-2, the two distal pairs close together, the proximal at beginning of second quarter of segment; metatarsus, ventral only, 0-2-2. Second leg differs from first in having tibia ventral 1r-1r-2, (male) or 1r-0-2 (female); tibia prolateral, male only, 1-1 (both small); metatarsus, female only, with 1 prolateral distal. Third leg, femur, dorsal 0-1-1-1, prolateral distal 2 (male), or 1 (female); tibia prolateral 0-1 (male) or none (female); retrolateral 0-1; ventral 0-0-2 (male) or 1p-1p-2 (female); metatarsus prolateral distal 2, retrolateral distal 2, ventral distal 2. Fourth leg, femur as in third; tibia prolateral none (male), or 0-1 (female); retrolateral 0-1 or none (variable on two sides); ventral 1p-0-2 or 1r-1r-2 or 0-0-2 (variable on two sides); metatarsus prolateral distal 0-1, sometimes in female only 0-2, the second weak; ventral distal only 2, on one side of female 0-2-2.

*Abdomen*: Ovate in both sexes, the breadth about 70-75% of length, widest near middle.

*Palp*: Femur strongly curved; tibia more than one-half length of patella; tibia with a retrolateral apophysis which tapers to a blunt, slightly recurved point. Embolus tapering from a broad base to a curved and slender tip.

*Epigynum*: An anterior pair of bodies well separated, a posterior pair contiguous; marginal notch deep and narrow.

### Measurements.

Male holotype. Total length in alcohol 4.51 mm.; carapace length 2.4, breadth 1.6, height 1.0; ocular quadrangle length .79, breadth 1.4; diameter AME .43, ALE .21, PME .03, PLE .19; clypeus height .05; basal segment of chelicera 1.37; patella breadth, 1st leg, .31, 4th .24.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.3 | .85 | 1.0 | .72 | .44 | 4.3 |
| 2 | 1.1 | .58 | .62 | .62 | .41 | 3.3 |
| 3 | 1.1 | .48 | .55 | .68 | .34 | 3.2 |
| 4 | 1.2 | .55 | .82 | .75 | .34 | 3.7 |
| Palp | .79 | .27 | .17 | — | .58 | 1.8 |

Female paratype. Total length in alcohol 4.68 mm.; carapace length 2.05, breadth 1.54, height 1.03; ocular quadrangle length .83, breadth 1.4; diameter AME .43, ALE .21, PME .03, PLE .19; clypeus height .05; basal segment of chelicera .72; patella breadth, 1st leg, .34, 4th .26.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.1 | .65 | .68 | .55 | .38 | 3.4 |
| 2 | 1.2 | .51 | .85 | .72 | .38 | 3.7 |
| 3 | 1.2 | .51 | .79 | .68 | .34 | 3.5 |
| 4 | .92 | .55 | .55 | .48 | .34 | 2.8 |
| Palp | .55 | .24 | .24 | — | .38 | 1.4 |

BEHAVIOR.

*Locomotion*: Compared with *Ashtabula*, this *Sassacus* is somewhat more a jumper and walker, less a scurrier; also it palpates the ground far less with the first legs and palps. Compared to the spiders of the *Plexippus* group, however, it is a poor and reluctant jumper.

*Courtship Display*: *Stage I.* Male follows female about, the carapace moderately elevated and the first legs raised at a wide angle to each other; frequently lowered; the abdomen hangs down and is trailed inconspicuously from side to side with sideling. Display tends to be in a wide semi-circle around female, once her attention has been attracted. The long chelicerae are folded but held out laterally (when not displaying they are held at right angles to each other), and the palps extend straight out also, in contrast to their usual resting position when they hang over chelicerae. With increasing stimulation, zigzagging becomes more pronounced and a slow rocking is involved, the carapace and abdomen held stiffly and rocking as a unit. Stage II is usually attained within three to five minutes by couples of low threshold to display stimuli, and consists of the first legs thrust out in front, clear of the ground.

*Threat Display*: *Stage I.* Indistinguishable from Stage I of courtship, except that no rocking is involved. *Stage II.* It is only in the rare occurrence of this stage that the chelicerae blades are unsheathed; when two opponents are practically touching the first legs are brought upright, from the obliquely outward display position, and simultaneously the chelicerae blades are extended straight out in front, at right angles to the basal segment, which is maintained in the horizontal position typical of display. In each of the dozen or so observed encounters that reached this stage, one or the other male usually backed off promptly at this point; more rarely there was a brief tangle which ended without apparent injury. Usually one or both males retreated before reaching Stage II.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from herbs, shrubs and low trees.

*Affinities*: This species appears exceedingly close to *S. arcuatus* Simon, 1902, from Teffe, in the Amazon region. From the brief description, the only apparent differences are slight distinctions in the abdominal markings and the absence, in the present form, of a yellow spot on the palp femur.

*Material*: A total of 5 adult males and 5 adult females have been preserved in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 45451. Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 1, 1945.

PARATYPE: Female. Cat. No. 45452 Department of Tropical Research, New York Zoological Society; same locality as holotype (with which she mated); July 1, 1945.

The name *flavicinctus* is proposed in reference to the yellow bands characterizing the male.

**Sassacus ocellatus** sp. nov.

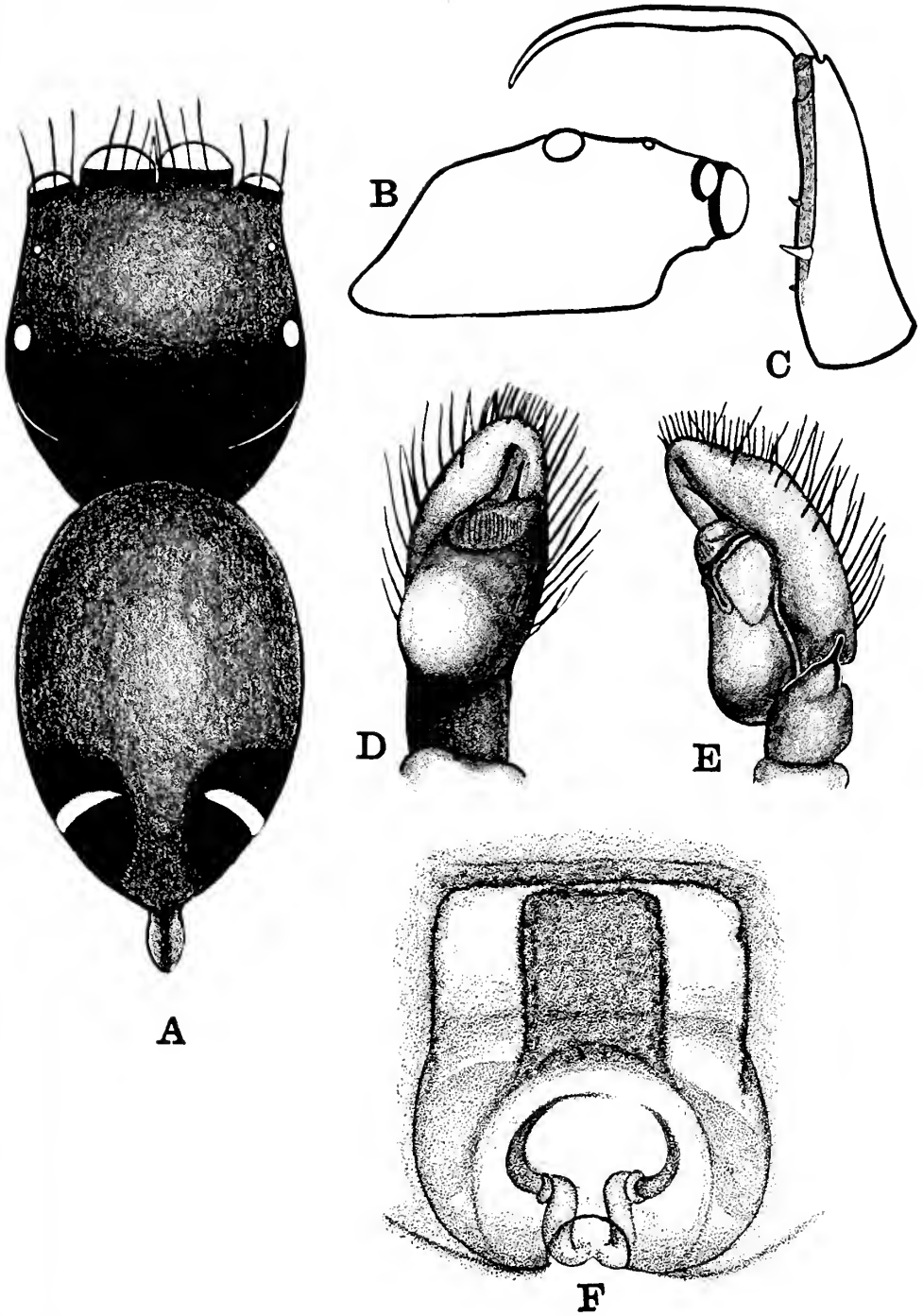
(Text-fig. 6).

*Diagnosis*: Both sexes iridescent green above, with a pair of black spots, each crossed by a white bar, near tip of abdomen. Chelicera of male strongly produced, the promargin with two well-separated teeth in proximal half, opposed by a single large tooth on retromargin. Spines of first tibia 2-2-2. Tibial apophysis of palp strong, simple, tapering, tip straight; embolus tip straight.

COLOR.

*Color in Life*: Adult male. Cephalothorax: Integument of carapace black; ocular region with a number of long bristles and completely covered with iridescent green scales which extend a little below it on sides and thoracic region. A broad band of white hairs, starting below PME on side of carapace, extends forward across clypeus. Palps, mouthparts and first legs jet black; other legs brown; two narrow, conspicuous stripes of white scales extend along anterior and posterior sides of first patella, tibia and base of metatarsus. These scales, although progressively fewer posteriorly, are present on anterior sides of all other legs, as well as on posterior sides of second legs. Sternum black. Abdomen entirely covered above, except as hereafter noted, with iridescent green scales, larger than those on carapace. On dorso-lateral surface on each side of posterior third is a large spot of velvety black scales, each with a narrow cross-bar of white scales from one-third to two-thirds of the way to its posterior edge. Around the entire abdomen laterally is a narrow band of iridescent green, confluent except in region of spot, with the dorsal green. Venter black.

Adult female. Cephalothorax: carapace as in male, with the addition of a narrow submarginal border of white scales continuing almost as far as pedicel. Entire face, around eyes, with more white scales and hairs than in male. Chelicerae black with a few white hairs basally; palps translucent brown barred narrowly with darker on joints, and with a few white hairs on patellae. All legs translucent brown except first femora, which are almost black. Sternum black. Abdomen as in male, except that there is a faint an-




TEXT-FIG. 6. *Sassacus ocellatus*. A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, chelicera, ventral view; **D**, palp, ventral view; **E**, same, ectal view. **F**, paratype ♀: epigynum.

terior band of white scales, dying out laterally in variable faint spots, while the white cross-bars on the posterior black spots tend to be on the latter's anterior margin.

*In alcohol* the iridescent green completely vanishes, the scales appearing dull yellowish or brownish; the abdominal black spots with white cross-bars are discernible, but far less distinct than in life, the anterior part of the spot tending to disappear altogether. As usual, the black integumentary areas fade to brown.

STRUCTURE.

Essentially as in *S. flavicincta* except in the following respects: carapace lower, its height less than half carapace length in both

sexes, lower in male than in female. *Chelicera* of male even longer in some specimens, but varying in individuals; basal segment in holotype is 5/6 of carapace length; promargin with two small teeth well separated, along proximal half of groove; opposite their interspace, on retromargin, is a single, much larger, conical tooth. *Tibial indices*: Holotype male, first leg 21, fourth leg 19; paratype female, first leg 25, fourth leg 19. See Table VI for formula.

TABLE VI.

*S. ocellatus*: Leg Formula.

| | 1 | 4 | 2 | 3 |
|---|---|---|---|---|
| Male holotype | 1.9 | 1.5 | 1.4 | 1.2 |
| | 1 | 4 | 2 | 3 |
| Female paratype | 1.7 | 1.7 | 1.3 | 1.3 |

*Spines*: As in *flavicinctus*, but with first tibial ventral 2-2-2, not 1r-2-2, and with spines on posterior legs somewhat fewer, viz.: Second leg: Male, tibia prolateral 0, not 1-1; female as in *flavicinctus*. Third leg: Male, femur prolateral distal 1, not 2; female, prolateral 0, retrolateral 1; tibia 0 in both sexes, not with a few pro- and retrolaterals and ventrals; metatarsus (both sexes) pro- and retrolateral distals each 1, not 2. Fourth leg (both sexes): Femur prolateral 1 not 2; tibia, ventral distal only 1p in male, 0 in female; metatarsus, as in third leg, but with traces of another lateral distal pair (very weak), similar to those in *flavicinctus;* especially noticeable in female.

*Palp*: Tibial apophysis and embolus both straight, not curved. *Epigynum*: Radically different from that of *S. flavicinctus* (see figure); marginal notch broad and shallow.

MEASUREMENTS.

Male holotype. Total length in alcohol 3.3 mm.; carapace length 2.1, breadth 1.5, height .79; clypeus height .07; basal segment of chelicera 1.8; patella breadth, 1st leg .34, 4th leg .22; length of abdomen 2.2, breadth 1.4.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.2 | .72 | .92 | .65 | .44 | 3.9 |
| 2 | .89 | .55 | .62 | .58 | .38 | 3.0 |
| 3 | .82 | .44 | .51 | .48 | .38 | 2.6 |
| 4 | .99 | .51 | .68 | .65 | .38 | 3.2 |
| Palp | .82 | .55 | .14 | — | .58 | 2.1 |

Female paratype. Total length in alcohol 5.0 mm.; carapace length 1.7, breadth 1.3, height .72; clypeus height .10; basal segment of chelicera .58; patella breadth, 1st leg .31, 4th leg .21; length of abdomen 3.3, breadth 2.1.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | .85 | .62 | .62 | .48 | .34 | 2.9 |
| 2 | .68 | .48 | .41 | .38 | .31 | 2.3 |
| 3 | .68 | .41 | .41 | .44 | .31 | 2.3 |
| 4 | .89 | .48 | .65 | .55 | .37 | 2.9 |
| Palp | .44 | .21 | .21 | — | .34 | 1.2 |

BEHAVIOR.

*Locomotion*: About midway between *Ashtabula* and *S. flavicinctus*. Its usual progress is a rapid scurry, jumping only when necessary, the first legs held forward, usually scarcely touching the ground, the palps held just clear of it. During the infrequent pauses, the first legs and palps are raised in the air and waved up and down; after which both sets of appendages sometimes palpate the ground itself.

*Courtship Display*: *Stage I.* Carapace scarcely elevated, first legs held up at about right angles to each other, and brought to ground again during the jerking, zig-zag approach to female. The long chelicerae are sheathed, the palps hanging quietly over them in the normal resting position, except for occasional vibration. Approach to the female is often quick and direct after the preliminary zig-zags. The most interesting phase may or may not be included; it consists of posing for a few moments, motionless, the legs elevated, and the abdomen twisted slightly to one side or the other; once the female was seen to perform the same motion, although that courtship was not completed. The relatively short abdomen was never swung far to the side as in the elongate *Ashtabula*, and the black, white-barred terminal spot could not have been in full view. In the single courtship which ended in actual mating, this phase was altogether omitted. *Stage II.* This was often reached within three minutes; in one case mating followed five minutes after display began. It did not differ from that of *flavicinctus*.

*Threat Display*: True fighting frequently takes place in this species and even when inter-male display ends in mere threat, the chelicerae are always more or less unsheathed, which never happens in courtship. The behavior otherwise is similar except that I observed little or no trace of the side-swinging of the abdomen. During actual battle the first legs are raised directly overhead, and the palps extended laterally, widespread, out of the way; the wide-open chelicerae are opposed to those of the opponent. The two may then push back and forth for seconds, until one of the pair retreats or is bitten.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always shaken from herbs, shrubs and low trees.

*Affinities*: The abdominal markings are somewhat similar to those of *S. aurantiacus* Simon, 1902, from Para, Brazil, known only from the briefly described female. The present species has a full set of 2-2-2 spines on the first tibia, instead of 1p-2-2, in both sexes.

*Material*: A total of 11 adult males and 9 adult females have been preserved in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 461204, Department of Tropical Research, New York

Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; March 27, 1946.

PARATYPE: Female. Cat. No. 481560, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 17, 1948.

The name *ocellatus* is proposed in reference to the eye-like abdominal markings.

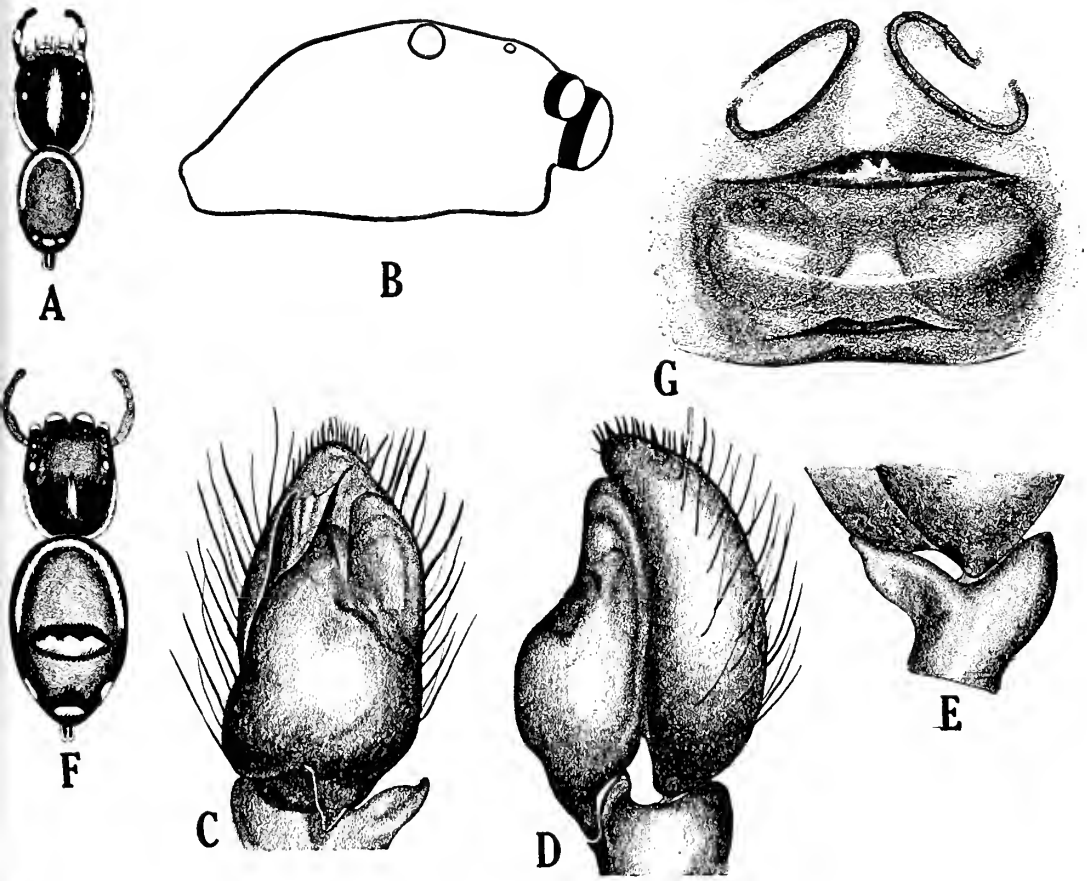
### ***Phiale flammea*** sp. nov.

(Text-fig. 7).

*Diagnosis*: All carapace bands in both sexes creamy yellow. Male: Carapace markings broad, including submarginal and clypeal bands and mid-dorsal stripe; no spots near PME. Abdomen above bright rufous with white markings; median spot absent, although a faint cross-bar may be present or absent beneath rufous scales; no terminal hook on antero-lateral band; three terminal spots. Palp with tibial apophysis stout, truncate; bulb strongly bilobed; lateral process of embolus shorter than and widely separated from embolus proper. Female: Carapace markings less extensive than in male. Abdomen with reddish scales ranging almost to black; anterior abdominal band as in male; strong, post-median cross-bar and terminal spots present. Epigynum with two strongly chitinized, external cross-bars.

COLOR.

*Color in Life*: Adult male. As in Chickering's description of *P. aliceae* in alcohol (1946, p. 207), except as follows: Cephalothorax: Integument of carapace, mouthparts, palps and first legs (except metatarsus and tarsus) black, not dark brown; integument of other legs translucent, medium brown. All carapace scale-hair bands distinctly buffy yellow; anterior eyes rimmed with rust; clypeus with a strong band of creamy yellow scale-hairs, instead of only "a fringe of yellowish bristles;" palp femur with dorsal scale-hair patch as in *aliceae;* a patch of white-scale hairs on proximal anterior face of first metatarsus and tarsus; variable numbers and arrangements of similar scales, diminishing posteriorly, on other segments of other legs. Abdomen: Dorsum in full sunlight often matches the flame scarlet of Ridgway; other individuals tend to orange rufous. As in *aliceae,* white markings consist of a simple anterior band extending dorso-laterally more than halfway to spinnerets, and ending without a hook-shaped inward curve




TEXT-FIG. 7. *Phiale flammea.* A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, palp, ventral view; **D**, same, ectal view; **E**, same, tibial apophysis. F, G, paratype ♀: **F**, carapace and abdomen, dorsal view; **G**, epigynum.

(as is characteristic of *P. dybowskii*, for example); usually it ends abruptly; sometimes there is a very slight inward curve. The "narrow, light-colored central bar" of *aliceae* is invisible in live specimens though it sometimes shows in preserved examples, beneath the rufous scales. Three small white terminal markings, in the form of spots or short bars, as in *aliceae;* carapace stripe easily rubbed, often small in preservative.

Adult female. Exceedingly variable, both in the pattern of white and dark scales, and in the vividness of the reddish abdominal markings; the individuals are separated with difficulty in pattern from at least two other species occurring typically on the lower slopes of the same mountain range. They differ from the male as follows: Cephalothorax: buff stripe and bands of carapace—median, submarginal and clypeal—much less extensive; sparse rusty hairs usually present on and around ocular quadrangle; anterior eyes rimmed with yellowish-white, not rust; some buff hairs on face below ALE; palps translucent buffy yellow, not black, and lacking buff scales; first legs black only on femur and patella; white hairs and scales of all legs reduced or absent. Abdomen: Red of dorsum exceedingly variable, practically always less bright than in male, sometimes almost black. A strong post-median, black-bordered crossbar of white scales always present, but of variable length and breath, sometimes confluent with ends of anterior dorso-lateral band, which is as in male; posterior spots present as in male, but of more variable size and shape, sometimes partly confluent.

### Structure.

This species is so close to *P. aliceae* (known only from holotype male) that no significant structural differences emerge from a comparison of Chickering's description with our species, except for minor spine and palp differences as given below. The females are closely similar to the males in structure, except for the usual leg differences, and for the absence of the small hooked maxillary process.

*Spines* (both sexes): Differ from *aliceae* as follows: First leg, Female: Patella prolateral 0, not 1. Second leg, both sexes: Tibia prolateral as in first (1-0-1, not 1-1-1), ventral apparently consistently 1r-2-2, not variable; metatarsus male, prolateral distal 0, not 1, but this spine present in female. Third leg (female only): Femur prolateral distal only 2, not 1-2, retrolateral 1, not 2; tibia dorsal 0, not 1; metatarsus with slight irregularities on one side of paratype female only, retrolateral 0-1-2, not 1-1-2, ventral 1p-1p-2, not 0-2-2. Fourth leg: Femur (both sexes) prolateral and retrolateral distal respectively 0 and 1, not each 2; male tibia as on right side of *aliceae* holotype, female dorsal 0, not 1.

*Palp*: Differs from that of *aliceae* in its relatively greater breadth and in the character of lateral process of embolus; in *flammea* the two parts are much farther apart, though connected by a thin, horny plate; also, the lateral process is much shorter than embolus proper, and scarcely curved distally.

*Epigynum*: Confusing, as usual in this genus, on account of the frequent secretion of gummy matter which obscures and distorts the structure. Always distinct, however, are two strongly chitinized transverse, lip-like structures, one between the two pairs of subdermal bodies and one near posterior border.

### Measurements.

Male holotype. Total length in alcohol 4.6 mm.; carapace length 2.7, breadth 1.9, height 1.1; clypeus height .19; basal segment of chelicera .89; patella breadth. 1st leg, .41, 4th .28; length of abdomen 1.9, breadth 1.4.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.8 | 1.1 | 1.7 | 1.1 | .68 | 6.4 |
| 2 | 1.3 | .75 | .89 | .79 | .48 | 4.2 |
| 3 | 1.5 | .79 | .85 | 1.1 | .55 | 4.8 |
| 4 | 1.6 | .75 | 1.2 | 1.3 | .55 | 5.4 |
| Palp | .85 | .24 | .24 | — | .82 | 2.2 |

Female paratype. Total length in alcohol 5.1 mm.; carapace length 2.5, breadth 1.7, height 1.1; clypeus height .07; basal segment of chelicera .85; patella breadth, 1st leg .40, 4th .31; length of abdomen 2.6, breadth 1.7.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.2 | .85 | .89 | .65 | .51 | 4.1 |
| 2 | 1.1 | .65 | .65 | .62 | .48 | 3.5 |
| 3 | 1.3 | .72 | .79 | .82 | .55 | 4.2 |
| 4 | 1.4 | .72 | .99 | 1.1 | .62 | 4.8 |
| Palp | .65 | .27 | .31 | — | .55 | 1.8 |

Tibial indices: Holotype male first leg 15, fourth leg 14; paratype female, first leg 23, fourth leg 18. See Table VII for formula.

TABLE VII.

*P. flammea*: Leg Formula.

| | | | | |
|---|---|---|---|---|
| | 1 | 4 | 3 | 2 |
| Male holotype | 2.4 | 2.0 | 1.8 | 1.5 |
| | 4 | 1 | 3 | 2 |
| Female paratype | 1.9 | 1.6 | 1.7 | 1.4 |

*Locomotion*: Primarily a runner, although jumps are undertaken over gaps without hesitation. The first legs take little part in locomotion and are habitually waved up and down during the pauses.

*Courtship Display*: *Stage I.* Carapace elevated high; abdomen hangs down, usually touching ground and leaving a silk thread. First legs raised at 45° angle with each other and the ground. Female approached in zigzag spurts, as the carapace is rocked from side to side, sinking alternating almost to the ground, from right to left. Palps irregularly vibrated up and down. Pursuit of female plays an important part in early stages,

but once female's attention is gained, she usually watches with first legs elevated and palps vibrating rapidly.

*Stage II.* Male abruptly crouches almost on ground, when two inches or less from female; his legs far outstretched in front, almost parallel, he approaches her directly with crawling motion, the palps vibrating in unison and entire body quivering. The remarkable point about Stage II in this species is that it begins at such a relatively long distance from the female.

*Threat Display*: As in Stage I of courtship, except that the palps are held quiet most of the time, the creamy yellow patch of the curved femur continuing that of the clypeus in an unbroken line. When approach is very close the chelicerae are opened and the first legs spread more widely, often actually touching those of the opponent. The bouts are always brief and I have never seen damage inflicted.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around Rancho Grande. Always taken on herbs, shrubs or small trees.

*Affinities*: The closeness of this species to *P. aliceae* has already been noted. When adequate material is taken from intermediate localities, it seems likely that the distinctions will prove to be of only subspecific importance.

*Material*: A total of 14 adult males and 20 adult females have been preserved. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 481561, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters, cloud forest; July 25, 1948.

PARATYPE: Female. Cat. No. 45453, Department of Tropical Research, New York Zoological Society; same locality as holotype; July 26, 1945.

The proposed name *flammea* refers to the color of the male dorsum.

### ***Mago dentichelis*** sp. nov.

(Text-fig. 8).

*Diagnosis*: Carapace of unrubbed individuals with a median white stripe enclosing a central black spot. Male chelicera with tooth on external border; four or five teeth on inferior margin; two or three teeth, plus a series of denticles, on superior margin; tibia of palp with three unequal apophyses; epigynum with a median, rounded, superficial, pale anterior body.

#### Color.

*Color in Life*: Adult male. Cephalothorax: Carapace integument black, practically naked except for a conspicuous median stripe of white scales enclosing, behind level of PLE, a central black spot. The stripe begins behind AME, or near level of PME, widens to encompass the spot, then narrows once more, ending at or behind middle of thorax. White of spot region sometimes extending laterally as a short cross-bar. Sparse chestnut and black hairs scattered on ocular quadrangle near dorsal eyes, and around AME. The wide clypeus is black and completely naked; palps, mouthparts and first pairs of legs black, except for leg tarsi. These and entire third and fourth legs translucent brown, variably and faintly banded with darker near ends of segments. Palps and all legs, especially first two, with inconspicuous white scale-hairs on antero-dorsal surfaces near joints. Sternum black. Abdomen: Pattern of dorsum very variable, formed chiefly of short hairs or scale hairs, brown mixed with gray and white areas. Usually a white lyre-shaped anterior marking—a strongly curved band with a short median basal stripe—is distinct; this is followed by several pairs of faint chevrons and some white lateral streaks and spots. The most constant markings are a pair of white terminal spots. Venter black with a pair of pale faint longitudinal stripes in middle; buff hairs rather thickly scattered over entire surface.

Adult female. Dorsal markings very similar to those of male, but posterior abdominal spots less distinct and more variable. Palps pale, translucent horn; first and second legs banded, not black; white scale-hairs on appendages almost or completely absent, though short yellowish hairs sometimes present near joints.

*In alcohol*, the distinctive markings usually disappear from both sexes.

#### Structure.

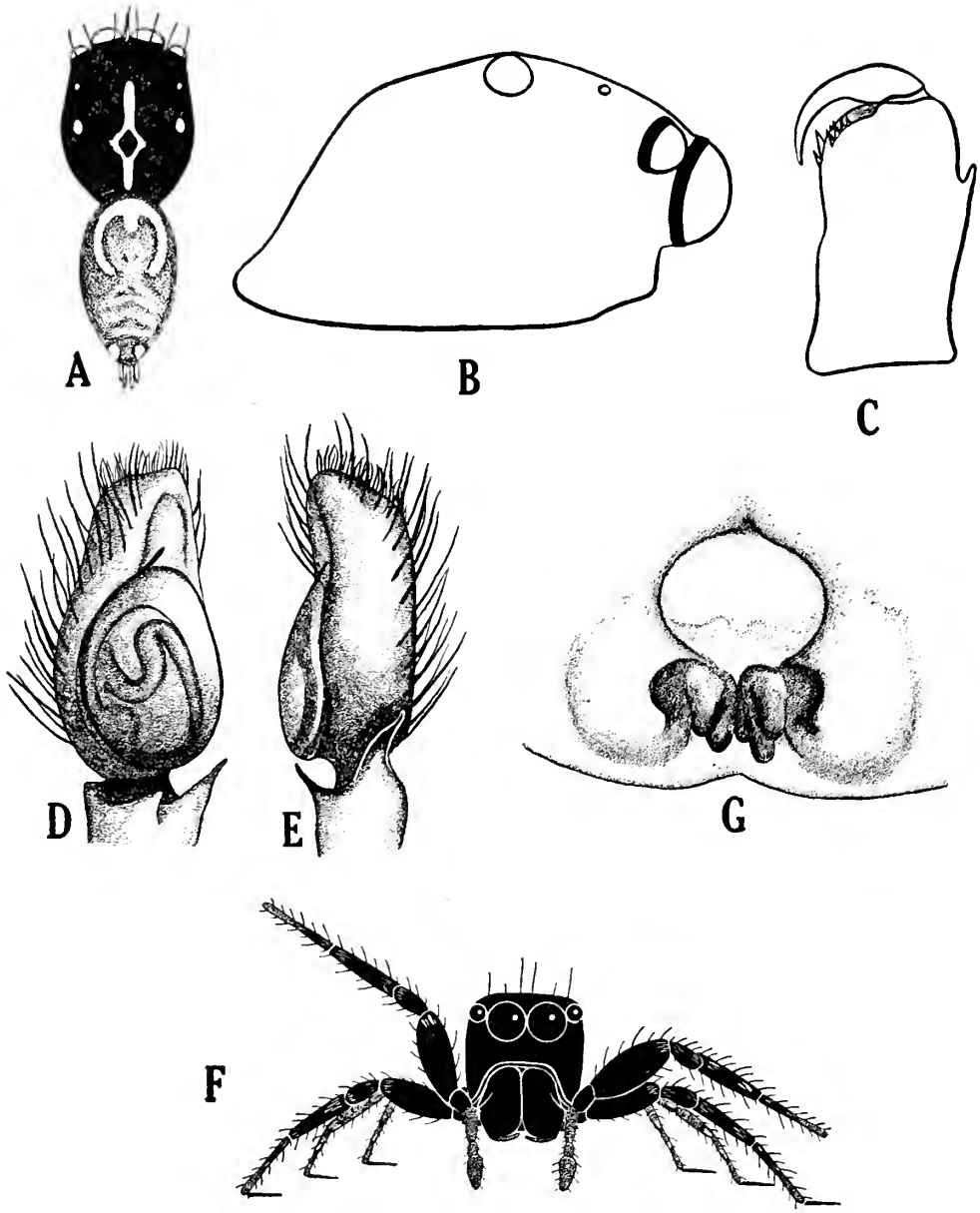
The characteristics below apply to both males and females unless otherwise specified; percentages approximated; measurements of types given on p. 51.

*Carapace*: Height 57% of carapace length; profile rises behind AME, gently convex, to PLE; anterior half of thorax descends very gently, posterior half abruptly; widest at level of PLE, 1.3 times height, 73% of length; total length of eye group slightly more than half carapace length. A distinct longitudinal thoracic groove, centering at level of posterior margin of PLE.

*Eyes*: Length of ocular quadrangle about two-thirds of breadth, its sides almost parallel but width at ALE slightly greater than at PLE; carapace extending well beyond PLE at their level; PME slightly closer to ALE than to PLE. Diameter of AME 23% of carapace length; ratio of eyes, holotype: AME : ALE : PME : PLE :: 100:46:14:40. AME practically contiguous, separated from ALE, which are slightly recurved, by about a tenth of their diameter.

*Clypeus*: Height 52% of AME diameter in male, 28% in female.

*Chelicerae*: Not produced, vertical, parallel. Length of basal segment less than 30% of carapace length. Male with a strong tooth about middle of external border. Promargin




TEXT-FIG. 8. *Mago dentichelis*: A-E, holotype ♂: **A**, carapace and abdomen, dorsal view; **B**, carapace, lateral view; **C**, chelicera, ventral view; **D**, palp, ventral view; **E**, same, ectal view; **F**, threat display. **G**, paratype ♀: epigynum.

with two (rarely three) moderate-sized teeth at proximal angle, the distal the larger; distal to these is a series of minute granular teeth, numbering three or more. Inferior margin usually with four, sometimes five, contiguous, well developed teeth.

*Maxillae*: Less than twice as long as wide, outer distal angle little dilated.

*Lip*: Length and breadth similar; posterior margin slightly convex, about equal in breadth to anterior margin of sternum.

*Sternum*: Breadth three-fourths of length in male, two-thirds in female, widest at anterior margin of third leg. Anterior border concave, posterior broad and convex, ending before anterior half of fourth coxae; posterior half of latter separated by about an eighth of their diameter.

*Legs*: Tibial indices: Holotype male, first leg 17, fourth 29; paratype female, first leg 23, fourth 16. First femur, patella and tibia moderately enlarged, less so in second leg. See Table VIII for formula. All legs with little hair.

TABLE VIII.

*M. dentichelis*: Leg Formula.

| | | | | |
|---|---|---|---|---|
| | 1 | 4 | 3 | 2 |
| Male holotype | 2.1 | 2.0 | 1.9 | 1.9 |
| | 4 | 3 | 1 | 2 |
| Female paratype | 1.9 | 1.8 | 1.7 | 1.6 |

*Spines*: First leg: Femur dorsal 0-1-1-1, prolateral distal only 2; patella prolateral only 1 or 0; tibial prolateral 1-0-1 (both weak), or 0-0-0; retrolateral 0; ventral, 1r-1r-2, or 2-2-2; metatarsus ventral only 2-2. Second leg: Femur dorsal 0-1-1-1, prolateral distal only 2, retrolateral female only 1; patella prolateral 1 or 0; tibia prolateral 1-1-1 or 1-0-1, retrolateral 0, ventral 1r-2-2; metatarsus ventral only 2-2. Third leg: Femur dorsal 0-1-1-1, prolateral 1 or 2, retrolateral 1 or 0; patella prolateral 1, retrolateral 1; tibia prolateral 1-1, retrolateral 1-1-1; ventral 1p-0-2; metatarsus prolateral 1-1, retrolateral 1-2, ventral 2-2. Fourth leg: Femur dorsal 0-1-1-1, prolateral 1, retrolateral 1; patella prolateral 1, retrolateral 1; tibia prolateral 1-1-1 or 1-1, retrolateral 1-1-1, ventral 1p-2; metatarsus prolateral 1-1, retrolateral 1-1-2, ventral 1p-2.

*Abdomen*: Rather narrowly ovate, widest near middle.

*Palp*: Femur slightly curved, tibia about 70% length of patella; tibia with three apophyses, one small and ventral, one long and tapering, external to the first, and the third still larger, sinuously tapering, dorso-lateral. Embolus short and simple.

*Epigynum*: A large, rounded, median, whitish anterior area, followed by a variable arrangement of four or five subdermal, near-median tubules, related to two less distinct, well separated oval bodies.

### Measurements.

Male holotype: Total length in alcohol 5.2 mm.; carapace length 2.6, breadth 1.9, height 1.5; total length of eye group 1.4; ocular quadrangle length 1.1, breadth 1.7; diameter AME .60, ALE .28, PME .09, PLE .24; clypeus height .31; basal segment of chelicera .99; sternum length .99, breadth .75; abdomen length 2.6, breadth 1.5; patella breadth, 1st leg, .41, 4th .39.

Leg Measurements, Male.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.6 | .96 | 1.4 | .99 | .58 | 5.5 |
| 2 | 1.4 | .89 | 1.1 | .92 | .58 | 4.9 |
| 3 | 1.6 | .75 | 1.1 | 1.1 | .48 | 5.0 |
| 4 | 1.5 | .68 | 1.2 | 1.2 | .62 | 5.2 |
| Palp | .89 | .38 | .27 | — | .68 | 2.2 |

Female paratype: Total length in alcohol 5.3 mm.; carapace length 2.5, breadth 1.8, height 1.4; total length of eye group 1.4; ocular quadrangle length 1.1, breadth 1.6; diameter AME .55, ALE .26, PME .09, PLE .24; clypeus height .15; basal segment of chelicera .79; sternum length .96, breadth .65; abdomen length 2.8, breadth 2.0; patella breadth, 1st leg .40, 4th .28.

Leg Measurements, Female.

| Leg | Femur | Pat. | Tib. | Metat. | Tarsus | Total |
|---|---|---|---|---|---|---|
| 1 | 1.3 | .79 | .96 | .72 | .38 | 4.2 |
| 2 | 1.3 | .79 | .85 | .65 | .44 | 4.0 |
| 3 | 1.4 | .79 | .92 | .89 | .51 | 4.5 |
| 4 | 1.5 | .65 | 1.1 | 1.1 | .58 | 4.9 |
| Palp | .68 | .41 | .34 | — | .38 | 1.8 |

### Behavior.

*Locomotion*: Not specially observed in this species; however, another *Mago* (undescribed) as well as *Hypaeus* sp. are both excellent jumpers. In these the repeated pattern of ordinary progress is a deliberate walk for two or three centimeters followed by a series of short jumps; the first legs take active part in the walking and jumping, and are never raised except during display.

*Courtship Display*: *Stage I*. Carapace elevated only enough so that the motionless, hanging palps clear the ground; first legs raised at a wide angle to each other (about 135°), the other legs extending far sidewards, the second pair slightly forward. Posing in this attitude is extended, but at intervals the first legs wave alternately up and down. Meanwhile the abdomen, which is held horizontally clear of the ground, is occasionally vibrated briefly up and down.

*Stage II*. First legs extend to front, usually not before female thrusts her first legs momentarily forward. Carapace and legs of male, in addition to the abdomen, twitch and jerk before he touches her.

*Threat Display*: Much more active than courtship, and in several respects quite distinct. *Stage I*: Carapace held moderately low, the abdomen either straight out as in courtship, or relaxed downward for silk attachment. First legs held with femur bent obliquely up, the other segments out; from that joint the two legs are waved up and down, usually in unison with each other, sometimes alternately. The palps hang down outside the closed chelicerae, as in courtship.

*Stage II*. The tempo and span of waving increases, the first legs almost meeting overhead at peak of display. Series of waves are punctuated by the rapid rubbing together of the first and second tarsi of each side, the second legs are braced somewhat forward, as in courtship, and are occasionally lifted briefly from the ground during waving.

*Stage III*. The two males oppose each other closely, the first legs straight overhead, practically or completely touching, the palps swung obliquely out, and the chelicerae opened wide and knocking against each other for seconds at a time. I have seen this stage reached only twice, no injury being inflicted either time. Only when one was retreating did the abdomen twitch very briefly, as in courtship.

*Habitat*: Known only from the montane cloud forest (about 3,600 feet) around

Rancho Grande, taken from vines on tree trunks, herbs and shrubs. Several specimens collected on upper Rancho Grande verandah, many yards from vegetation.

*Affinities*: Apparently related to Simon's briefly described *longidens* and *acutidens* from Brazil, although distinct in details of white markings, distal dentition of chelicerae and presence of three apophyses on palpal tibia.

*Material*: A total of 6 adult males and 11 adult females have been preserved in addition to a number of young. The following have been designated as types:

HOLOTYPE: Male. Cat. No. 45454, Department of Tropical Research, New York Zoological Society; Portachuelo, Rancho Grande, near Maracay, National Park of Aragua, Venezuela; 1,136 meters; cloud forest; June 6, 1945.

PARATYPE: Female. Cat. No. 45455. Taken near holotype, same locality and date.

The name *dentichelis* is proposed in reference to the large outer tooth of the chelicera.

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# 8.

## The Swifts of Rancho Grande, North-central Venezuela, with Special Reference to Migration.[1]

WILLIAM BEEBE.
*Department of Tropical Research, New York Zoological Society.*

(Plate I; Text-figures 1-3).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane cloud forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh water lake of Valencia, and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a 5-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe & Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were observed or taken in or over the montane cloud forest zone, within a radius of 1 kilometer of Rancho Grande.]

CONTENTS.



[1] Contribution No. 841, Department of Tropical Research, New York Zoological Society.

INTRODUCTION.

In all of South America there have been recorded (Peters, 1940) nine genera of swifts, divided into twenty species and a total of thirty-three kinds, including subspecies. In Venezuela Mr. William H. Phelps informs me there are six genera, of thirteen species of twenty kinds, if we include subspecies. Of these Venezuelan birds, within an area of less than one square kilometer with its center at Rancho Grande, I have recorded eight species of five genera; roughly eighty per cent. of the genera and sixty per cent. of the total Venezuelan species of swifts.

Late in the year 1937 Dr. Alexander Wetmore (Wetmore, 1939) spent some time collecting birds near Rancho Grande, and I quote the following notes concerning the swifts.

"In Tropical America swifts are tantalizing birds usually seen out of range . . . On November 4 at Rancho Grande several (*Chaetura brachyura*) circled out of range. This species appears very black as it flies overhead, so that at first glance it suggests the black swift (*Nephoecetes niger*), but a second look distinguishes it by the shorter, light-colored tail. The specimen taken, a male, measures as follows: Wing 118.7, tail 29.0, culmen from base 5.8, tarsus 11.8 mm."

Concerning *Streptoprocne zonaris albicincta*, he writes, "While I was collecting in Portachuelo above Rancho Grande on November 3, 6 and 10, groups of these large swifts dashed at intervals through the pass at lightning speed with a great rushing of wings. Occasionally I observed them circling in air."

These are, I believe, the only published notes on swifts in this restricted area.

My thanks go to Mr. William H. Phelps for the loan of skins of rare swifts, to Dr. Neal Weber for names of ants in the food of birds taken in 1948, and to Dr. J. Bequaert for the name of the feather fly found on *Aëronautes*. The three text-figures are the work of Miss Louise A. Moore. The photographs were taken by Miss Jocelyn Crane.

**Streptoprocne zonaris albicincta**
(Cabanis, 1862).

Giant White-collared Swift.

*Species Range*: Southern Mexico and the Greater Antilles, south over northern South America to British Guiana, north Matto Grosso and Peru; vertically to more than ten thousand feet in the Andes.

*Subspecies Range*: Five subspecies are recognized, of which *albicincta* occurs at Rancho Grande. Its range is extensive, from Honduras south to British Guiana, northern Matto Grosso and Peru, together with the islands of Granada and Trinidad. In Venezuela, Mr. Phelps records it as inhabiting the northern mountains.

*Field Characters for Sight Identification*: The most unmistakable species, distinguished by great size and white nuchal collar. It measures eight to nine inches in length, as compared to the five-inch average of the seven other species. *Panyptila* is the only other Rancho Grande swift with a white collar, but is about half the size of *albicincta*, and has a deeply forked tail. In young giant swifts the collar is reduced and indistinct in flying birds.

*Occurrence*: February 22 and September 9 are the earliest and the latest dates of our occupancy of Rancho Grande throughout three years. On both dates I recorded giant swifts within sight of the laboratory. Seldom did a day pass between these extremes when one or more did not come into view. Soon after we opened the station I ceased keeping detailed notes on these birds, as their visits seemed governed by no regularity.

They commanded attention under four separate conditions: (1) Almost daily either singly, but usually in small flocks, they hawked in the sky after insects, or (2) they flew headlong through Portachuelo Pass, low over the trees. (3) They entered rarely into the diet of a pair of resident bat falcons, *Falco albigularis*, and (4) on nights of storm, rain or neblina they occasionally struck against the windows of our lighted laboratory. Throughout the seven months during which we carried on our observations, there was no marked period of absence or extreme scarcity of these swifts. The breeding period must have occurred throughout part of this time but it was not noticeable in the rarity or abundance of individuals or flocks.

When it became evident that Portachuelo Pass was used as a migrating flyway on an unprecedented scale by other birds and by insects, I watched and noted these passing swifts for a period of several weeks, to see if there was any definite factor or sequence in their numbers or movements.

The daily, circling, feeding birds whose general direction was indefinite, varied their elevation, high or low, according to the volant stratification of edible insects. This proved to be definitely associated with the southward migration of insects of many orders through the pass. The swifts often joined flocks of swallows and even of large dragonflies where, on clear days, the migrants offered rich feeding in the area of the pass. At times of dense fog, high winds or lowering of temperature, the lessening or cessation of migration was correlated with a total absence of giant swifts. At Kilometer 15, a few kilometers south of the pass, I frequently saw flocks of these birds feeding high in air as I passed in the car; and to the north at Kilometer 30, six or eight pairs of the swifts were occasionally seen hawking about. Beyond these limits I saw no swifts.

Giant swifts are supposed to be normal inhabitants of strictly tropical regions. At Kartabo, British Guiana, at practically sea-level, I found them commonly in good-sized flocks, feeding on flying insects, especially in June, July and early August. During this season, mating flights of ants and termites were frequent.

From March 14 to July 17 I noted the following groups of giant swifts passing on twenty-three days at full speed south through the pass, all between 7 and 8:30 A.M. 1, 16, 6, 2, 11, 4 and 16, 3 and 7, 21, 12, 8, 16, 4, 1, 3, 1, 2, 14, 5, 4, 22, 19, 7, 5. All were in a terrific hurry, flying headlong, mostly low, their whistling wings just clearing the upper branches of bushes and trees. Throughout this period there were only five records of birds going north in early morning and few in numbers, 2, 6, 1, 9, 1. On June 24 at 3 P.M. 64 swifts rushed past over my head, headed full speed northward through the pass, just ahead of the onrolling fog.

On June 6, at five in the afternoon, a compact flock of 200 to 210 birds, at a moderate height, circled northward, giving the impression of a leisurely, non-feeding migration. On August 1, closely intermingling with about five thousand Argentine martins, *Phaeoprogne tapera fusca*, about 300 giant swifts accompanied the other birds, all at high speed. On August 8, 24 swifts passed low, going north through the pass.

The assumption of the northward return every afternoon and evening of these swifts through Portachuelo Pass seems justified because of the number of birds which long after dark on nights of storm or fog struck against the windows of our laboratory. These accidents occurred from 7:20 to 10:45 P.M. Fourteen birds struck in this way on eleven nights, April 9, 12, 18, May 4, 16, 23, June 10, 27, July 3, 4 and 6. On three nights two birds appeared. Four of the swifts which crashed the windows were skinned, three others were sexed, and the remaining seven escaped. All examined were males, and, of those examined, only the two birds which struck on April 9 were in full breeding condition.

Reviewing the records through the pass, it seems reasonable to assume a daily migration from some more northerly sleeping or breeding place, south to a feeding area, with the return very late in the afternoon or in the evening.

On May 4, four of these swifts fearlessly attacked a bat falcon, the male of the pair whose nesting we were watching. In connection with the attacking and repulsing of this hawk by the the swifts, we were interested to see the same individual falcon on three separate occasions return to his lofty perch with a dead swift. This is a remarkable feat when we realize that the latter is only about one-quarter less in size than the hawk. In an active flight dive the falcon could strike and capture any small bird it selected, but on a level the swifts were superior.

In the Santa Marta mountains of Colombia, about 575 kilometers west of Rancho Grande and at an altitude of 1,500 meters, this giant swift has been found nesting (Todd and Carriker, 1922). The account is as follows (p. 245): At the coffee plantation of Cincinnati, "on March 19, 1917, a colony of this large swift was discovered nesting in a shallow cavern behind a waterfall. The place was absolutely inaccessible, so that no idea of the number of nests could be had. Only one nest, which happened to be near the top, was secured, together with the occupants, . . . which had been stunned by the blasting, and proved to be an adult female and two recently hatched young. The nest resembled very closely that of the Chimney Swift, being composed of twigs fastened together with saliva. The birds entered and left the cavern by dashing through the curtain of water falling over the front of it. The altitude of the site was about 4,300 feet."

### Data on Collected Specimens.

For comparison I have included data concerning a female of this species taken many years ago at Kartabo, British Guiana.

| | | Lgth. | Wing | Tail | Grams Weight | Extent | Date |
|---|---|---|---|---|---|---|---|
| 30447 | male | 205 | 194 | 64 | 105.8 | 501 | July 3, 1945 |
| 30452 | male | 196 | 188 | 61 | 96 | 482 | July 3, 1945 |
| 31135 | male | 202 | 195 | 67 | 68.5 | 500 | April 9, 1948 |
| 31188 | male | 210 | 200 | 70 | 109.5 | | July 6, 1948 |
| 529 | female | 190 | 190 | 60 | 77.2 | | July 10, 1919 |

The relative discrepancies between length and weight are accounted for by the food. The stomach, with contents, of No. 31188 weighed 22.6 grams. Gross food content may be expressed as follows: 30447, crammed with ants; 30452, moderately filled; 31135, empty, after a day in cage; 31188, crammed with ants; 529, only about one-fourth filled with insects. Without exception, all the ants in the food were winged females.

*Detailed Food.*

30447: At least 800 ants of an undetermined species of *Azteca.*

30452: Several hundred females of *Dolichoderus* (*Monacis*) *debilis* Emery, and *Crematogaster* (*Orthocrema*) sp. A single female *Solenopsis geminata edwardi* Forel.

31135: Five female *Atta* sp. More than four hundred winged females of small ants.

31188: Stomach crammed with ants. (Weber).
Homoptera: Cicadellidae.
Diptera: fly fragments.
Hymenoptera: parasitic sp.
Hymenoptera: *Pheidole* sp.
Hymenoptera: *Atta sexdens* Linn. Four gasters and a hind wing fragment. A species known from Ciudad Bolivar, Venezuela, and south. Found in Eastern British Guiana, but apparently not in Venezuelan Guiana, the Orinoco Delta, N. W. District (B.G.); in these places replaced by *A. cephalotes* Linn.
*Azteca*?: wings.
*Camponotus* (*Myrmobrachys*) sp. Same as I took at 1,020 meters in Rio Porce, Colombia.
*Camponotus* (*Tanaemyrmex*) *substitutaus* Emery. Distribution: Central America to Paraguay. I have the same form from Kartabo, B. G.
*Camponotus* (*Myrmobrachys*) *crassus* Mayr. Distribution: South America.

529: Three beetles, three wasps, one hemipteron, three membracids, one tipulid, and upwards of two hundred female ants of six species.

It is significant that although swifts 30447 and 30452 struck the laboratory within six minutes of each other, yet their food was quite distinct, indicating very different feeding territories. Yet they were headed for the pass, focusing upon a sixty-foot-wide bottleneck.

### Individual Characters.

I find the following recorded concerning the Kartabo female, No. 529:

*Parasites*: Only a few bête rouge on the head feathers.

*Colors*: Bill black, face pale medici blue, iris light brownish-olive, legs and feet vinaceous slate.

*Eyelid*: Quite bare above. Below, a line of fifteen small feathers along rim. At posterior end of eye a small group of a dozen feathers, arranged in several rows.

*Oilgland*: Elongated, blunt, tapering, bare.

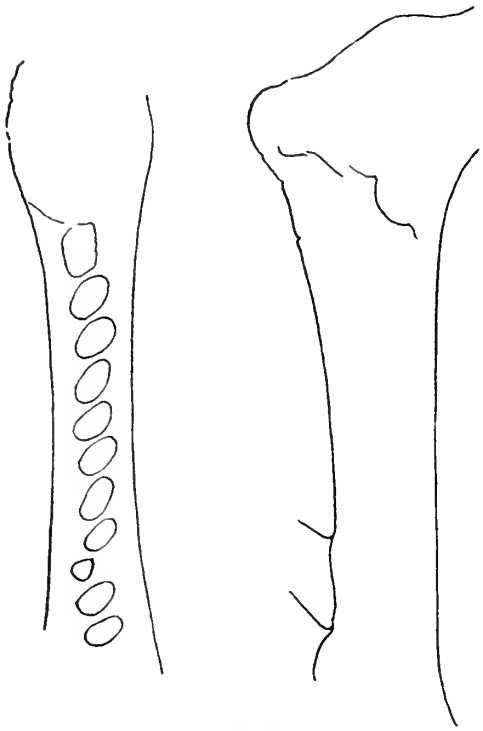
*Wing Graph*: Primaries

| | |
|---|---|
| 10th—152 mm. | 5th—111 mm. |
| 9th—155 " | 4th— 98 " |
| 8th—149 " | 3rd— 86 " |
| 7th—139 " | 2nd— 75 " |
| 6th—126 " | 1st— 62 " |

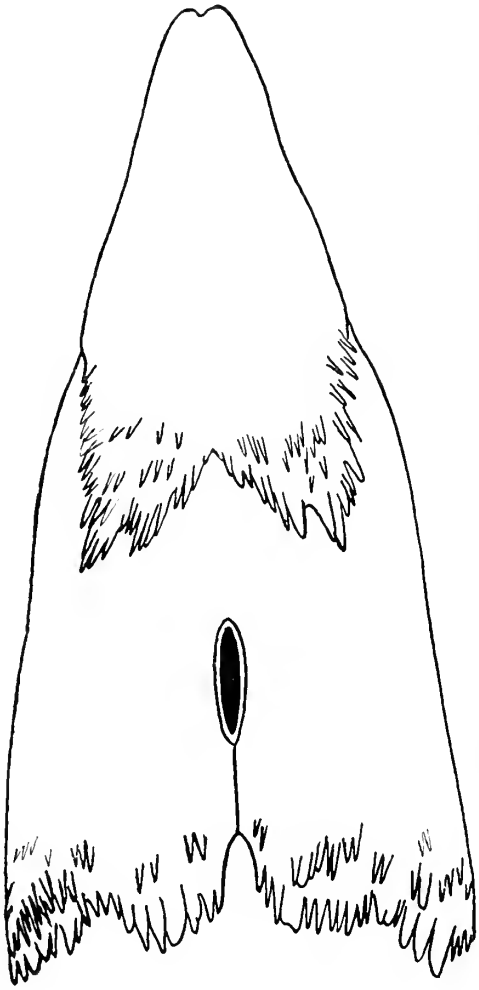
Secondaries

| | |
|---|---|
| 1st—49 mm. | 5th—53 mm. |
| 2nd—50 " | 6th—53 " |
| 3rd—52 " | 7th—49 " |
| 4th—54 " | 8th—42 " |

*Scalation*: Front of tarsus with an indistinct irregular line of ten, fleshy scales down the inner aspect. Inner, rear and outer sides of tarsus, bare, wrinkled skin, with no trace of scales.



TEXT-FIG. 1. *Streptoprocne zonaris albicincta* (Cabanis). Scalation of tarsus, front and side views.



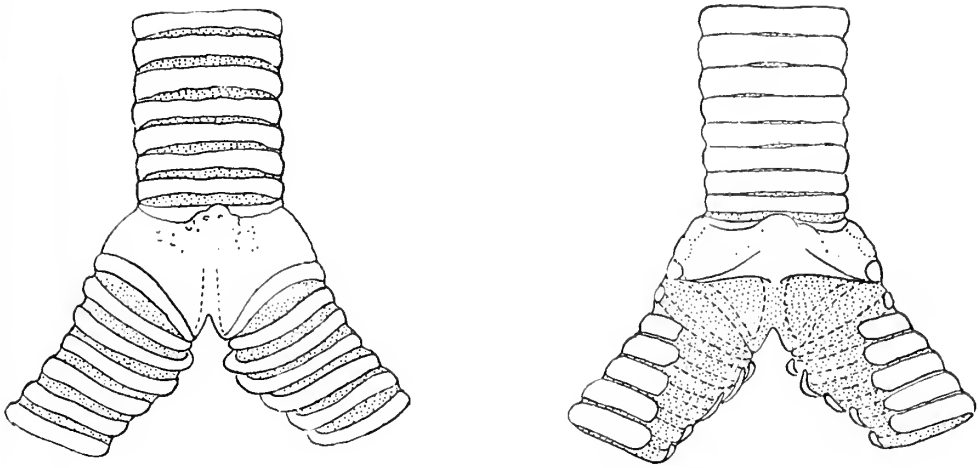
TEXT-FIG. 2. *Streptoprocne zonaris albicincta* (Cabanis). Tongue.

*Palate*: The palatine fissure begins well toward the front of the roof of the mouth, and divides in front. It is rather long (12.5 mm.) and is guarded by about a dozen pairs of teeth. Four-fifths of the way back there is a double-curved or angular transverse row of teeth, extending out at right angles on each side, with about twenty teeth on each side. The guardian, denticulated flaps end openly posteriorly, and just beyond is the very small tubal fissure. At the extreme posterior of the roof of the mouth is a transverse row of about twenty weak teeth.

*Tongue*: Narrow for a swift, and small for the size of the mandibular area. Greatest width of tongue 5.7 mm., length 10; greatest width of mandible 20 mm., length 26. Tongue fleshy, channelled toward the tip, sides somewhat sinuate, tapering slowly to two blunt tips. The two cornua are lined along the edge, both on inner and outer sides, with strong teeth. Smaller ones are scattered over the posterior surface of the tongue itself.

*Glottis*: A narrow ellipse on a low flat area, with inconspicuous unarmed rim. Posteriorly, there is an irregular transverse row of teeth, all large, flattened, sub-equal in size and numbering about fifteen on each side. Beyond these there arises a second irregular row. Most of the teeth, in a cleared condition, show stout, parallel-sided bases, and slender tips.

*Syrinx*: Swift No. 31135 (KOH No. 2589). Male. April 9, 1948. There is little change in the posterior tracheal rings except that the last eight are slightly narrowed with more even edges. The syrinx is a wide tracheobronchial collar of bone. Anteriorly the upper margin is level except in the center where an irregular, rounded projection overlies a segment of the last tracheal ring. This, like the rest of the syringeal collar is ossified and coarsely fenestrated. The anterior vertical width of the collar is 1.6 mm., its lateral, front to back, length is 3.3 mm. The lower border of the collar is formed by the closely-applied, strongly arched, upper bronchial



TEXT-FIG. 3. *Streptoprocne zonaris albicincta* (Cabanis). Syrinx, front and side views.

semiring. This semiring dips far down in front, forming an acute angle with the pessalus. The triangular space within this angle, as far anterior as the collar, is ossified, but without fenestration.

Posteriorly the tracheal rings are appreciably wider, with little more intervening membrane showing than the median, open notches. Two of the rings anastomose. The two lowermost rings are narrow and even as to outline.

Posteriorly, the syringeal collar is similar to its anterior half, with the difference that this aspect is flat and the median anterior projection is less pronounced. There is a faint but distinct indication that the present ossified syringeal collar was originally composed of two rings. The entire ventral syringeal aspect, bounded by the lower border of the collar, the pessalus and the first semiring is of course membranous. The free ends of the anterior semirings, joined by the tympaniform membrane, narrow rapidly posteriorly, until the ninth onwards become almost complete rings, thus forming the end of the membrane. There are about twenty-three bronchial rings, the second, third and fourth being somewhat longer, projecting slightly into the inner profile of the bronchi. From the eighteenth bronchial ring onwards there is a gradually increasing disintegration of the rings within the lung tissue, a thinning and irregular anastomosing of adjoining rings.

A drawing and description of the syrinx of the female No. 529, made thirty years ago, are similar to that of the present male except that posteriorly, the median protuberance is considerably larger, and extends forward over the last three tracheal rings.

### *Chaetura brachyura brachyura*

(Jardine, 1846).

Short-tailed Swift.

*Species Range*: Same as that of the subspecies below, with the addition of the Lesser Antilles.

*Subspecies Range*: Northern Venezuela and the Guianas to Trinidad and Tobago, south through eastern Ecuador and Peru to Matto Grosso and Pará.

*Field Characters for Sight Identification*: This is the smallest of the Rancho Grande swifts (length 100 mm.). On the wing it appears totally black, with conspicuous pale brownish-gray rump, tail-coverts and tail. The absence of gray on the underparts distinguishes it from the slightly larger *cinereiventris*.

*Occurrence*: By far the commonest swift at Rancho Grande, becoming really abundant after the rains began.

On clear days numbers were often seen feeding with swallows and other swifts, especially when migration of various orders of insects was in full swing. On partly cloudy days or when fog drifted up the lower valleys, these short-tailed swifts would swing through the pass in small or larger numbers.

There was none of the rather regular, southward, morning shift of the giant swifts. We saw this species every month from March to August, and on almost every clear day. It often flew in twos and threes, or again in flocks of considerable size. For three consecutive days, we were able to identify an individual trio. Two of the birds had recognizable gaps in their primaries due to molt, and these marked birds hawked on the north side of the pass, low in the gorge, throughout a three-day flight of termites, *Coptotermes testaceus*. On the third day an onrushing mass of dense fog drove these swifts away in the wake of eight turkey vultures hastening toward the upper zone of clear sunshine. The swifts did not return, and the next day the insect flight had ceased.

On July 9, 1948, we observed an unusual flocking, a migration of sorts; a fairly compact mass of considerably more than four

hundred of these swifts, circling, not feeding. As they approached the pass from the south, the flight changed to a more direct movement, and when siphoning through, all circling ceased, and the rush of wings was like a loud wind as the birds passed low and at great speed. The northern valley was partly filled with fog and the birds rose slowly above it, and before they passed from view, were again circling high in air as before. The general effect was of a maze of inorganic units, without volition, sucked by a wind through the narrow notch, and then sprayed out in a slower movement as the draught lessened. As a matter of fact, there was little or no breeze in the pass itself.

A spectacular coincidental sight of the same type of flocking of the same species is recorded in my notes on an identical July 9, but thirty-two years before, at Kalacoon, British Guiana. The note reads as follows: "An enormous flock of short-tailed swifts appeared over the forest at 9:30 this morning. There were certainly more than a thousand birds, all flying in a great circle, gradually attaining higher and higher altitude. They were massed so closely together that there seemed hardly room for any movement of the outspread, crescentic wings. The relative slowness of movement and the frequent effortless gliding indicated an upward surge of air. Through the glasses a scattering of equally small white-rumped swifts, *Chaetura spinicauda*, was clearly seen. The whole company vanished very high up and drifting southward."

Although these swifts showed little fear of the pair of bat falcons nesting near the laboratory, yet at least seven individuals fell victims to these hawks, and an eighth mangled swift found in the road near the nesting tree indicated an additional dropped item of diet. In this, as in other species, the swifts were able to evade the raptores when on the same aerial level. It was only when the hawks could go into a vertical dive that their speed made them almost unavoidable.

Two short-tailed swifts crashed against the laboratory windows on successive evenings, May 16 and 17, but one was able to fly away. The other was a male, breeding, with the stomach quite empty.

### *Chaetura cinereiventris lawrencei*

Ridgway, 1893.

Gray-breasted Swift.

*Species Range*: The range of the eight recognized subspecies extends from Nicaragua, Grenada, Tobago and Trinidad south to Venezuela, Colombia, Ecuador, Peru, central Brazil and Bolivia.

*Subspecies Range*: *lawrencei* occurs in Grenada, Tobago, Trinidad and the mountains of northern Venezuela.

*Field Characters for Sight Identification*: A small swift. Black, except for rump and all underparts, which are pale gray. When associated with *brachyura* and seen from above at a distance, the birds are much alike, the brownish shade of the rump of *brachyura* being hardly distinguishable. From below, the gray of *cinereiventris* instantly sets it apart.

*Occurrence*: This is not common at Rancho Grande, but was observed occasionally throughout May, June and July. Only once, on June 9, did an individual come to the laboratory windows. It clung for five minutes to the sill but evaded all efforts at capture.

On May 9, the male bat falcon caught a gray-breasted swift and plucked it. The female then gave it to her nestlings who tore it apart and ate it. As they pulled it apart I could distinctly see the mass of small ants which filled the stomach, together with two large abdomens of *Atta* queens which were eaten by the young birds.

### *Chaeturella rutila brunneitorques*

Lafresnaye, 1844.

Chestnut-collared Swift.

*Species Range*: Central Mexico, south through northern South America to Peru, the Guianas and Trinidad.

*Subspecies Range*: Southeastern Mexico, south to Colombia, Venezuela, Ecuador and Peru.

*Field Characters for Sight Identification*: A medium-sized swift, about five inches in length. It is the only species marked with chestnut; throat, breast and collar. This color is especially distinct when the birds are silhouetted against the foliage of the mountain jungle, but with glasses is conspicuous even when they are high in the sky.

*Occurrence*: The chestnut-collared swift was third in order of abundance at Rancho Grande, surpassed only by *Streptoprocne* and *Chaetura brachyura*. It was frequently seen shuttling back and forth through the pass, or hawking about on days of insect migration, associating with giant swifts or with swallows, mostly single birds or in small flocks. Occasionally they would race back and forth through the pass, yet the diurnal observations I was able to make showed no certain regularity of north or southward shift.

On the other hand sixteen birds struck against the laboratory windows and on three occasions, when no swifts actually flew against the glass, individuals were seen fluttering about among the bats within the area of illumination. This would indicate a daily, crepuscular northward migration, as in *Streptoprocne*, also perhaps to some roosting or breeding colony.

Support of the probability of such a migration is furnished by a chestnut-collared swift (31129) taken eight kilometers east of Rancho Grande. A reliable assistant, Pedro Infante, shot this bird January 8, before my arrival, on the Choroni road which parallels that from Maracay to Ocumare. He reported this swift as shot from a group of thirty to forty which, throughout October, November and December assembled every evening and spent the night clinging in a

compact mass to the vertical side of a rocky cliff near the road. All left at dawn. Thus we have evidence of a roosting colony at the same elevation as the pass, and, from the point of view of a volant swift, only a short distance away.

At Rancho Grande the meteorological conditions which induced the appearance of the swifts at the lighted windows were, high but dense clouds; low neblina fog with or without wind; precipitation, whether drizzle or pelting rain and with or without lightning. No birds ever came on clear nights, whether moon or starlighted, and no bird after 10 P. M.

There was considerable variation in the amount of chestnut on the plumage of these swifts, but the typical pattern was rich chestnut throat and breast with a wide collar extending over nape and hind neck. Two adult males had the chestnut reduced to a pectoral tinge, and several swifts on the wing were intermediate between these extremes. The only female examined (31143), an adult, showed no pigmental difference from a full-plumaged male, except that the under tail coverts were strongly edged with white.

Coleoptera spp., including a cerambycid.
Hymenoptera: *Camponotus* sp., fragmentary remains of several hundred.

31132: Half the meal composed of ants (Weber).
Coleoptera spp.
Hymenoptera: *Camponotus* sp., fragmentary.

31143: Dominant food, hundreds of small flying ants (Weber).
Hemiptera spp.
Coleoptera: cucurlionid.
Hymenoptera: *Pheidole* sp.
Hymenoptera: Very small dolichoderine fragments.

**Cypseloides cherriei** Ridgway, 1893.

White-spotted Swift.

*Former Records and Species Range*: Two swifts taken on Volcan de Irazu, central Costa Rica, were described by Ridgway in 1893. The type was thought to be a male; the second bird was uncertainly sexed as a female. The most noticeable character was "a large, sharply defined spot of silky white on each side of the forehead, immediately over the lores, and a short streak of the same color immediately behind the eye." A third specimen was reported (Zimmer, 1945) in a collection of birds from Colombia. This was taken at San Gil, Santander, and was also questionably sexed as a female.

This then, on February 26, 1948, was the summation of our knowledge of the white-spotted swift. The Costa Rican birds came from the same 10th degree of north latitude as Rancho Grande, but 1,800 kilometers west; whereas the Colombian swift, from 6 degrees, 33 minutes north latitude, was 750 kilometers to the southwest of our laboratory.

*Field Characters for Sight Identification*: The white-spot is a five-inch swift, appearing uniformly black, with a conspicuous, round, white spot between beak and eye. These spots stand out strongly whenever these birds are seen head-on in flight or from the side, giving a rather fantastic impression of a slightly misplaced pair of brilliant eyes.

*Occurrence*: At 9.30 o'clock in the evening

DATA ON CHESTNUT-COLLARED SWIFTS

| | | Lgth. | Wing | Tail | Grams Weight | Extent | Date |
|---|---|---|---|---|---|---|---|
| 30382 | male | 126 | 123 | 45 | 25 | | May 14, 1945 |
| 30382a | male | | | | | | May 14, 1945 |
| 30448 | male | 133 | 128 | 43 | 22.9 | 320 | July 3, 1945 |
| | Four swifts escaped | | | | | | July 3, 1945 |
| 31128 | male | 115 | 120 | 36 | | 292 | Mar. 23, 1948 |
| | One swift escaped | | | | | | Mar. 23, 1948 |
| 31131 | male | 130 | 120 | 43 | 21.5 | 295 | April 3, 1948 |
| 31132 | male | 128 | 120 | 45 | 21.5 | 302 | April 3, 1948 |
| | Four swifts escaped | | | | | | April 3, 1948 |
| 31143 | female | 122 | 125 | 43 | 19.5 | 305 | April 24, 1948 |

DETAILED FOOD.

30382: Many winged females of *Camponotus* (*Tanaemyrmex*) *coruscus* F. Smith; and *Solenopsis geminata edwardi* Forel.

30448: A series of winged females of *Crematogaster* (*Orthocrema*) sp.

31128: Stomach crammed with a mass of winged ants and small beetles. (Weber).
Homoptera: Cicadellidae.
Coleoptera spp., including a carabid.
Hymenoptera: parasitic sp.
Hymenoptera: *Crematogaster* ? wing.
Hymenoptera: *Solenopsis geminata* Fabr., widespread in the northern neotropics and replaced in the south by *saevissima* F. Smith, from the interior of British Guiana (Courantyne) and Brazil.
*Camponotus* sp.

31131: Food dominantly flying ants (Weber).
Hemiptera: wing.

of February 26, 1948, a white-spotted swift came to the windows of Rancho Grande and was caught. From this time until June 13 we captured or recorded eight others, making a total known of this unusual species of twelve individuals. The details of the nine Rancho Grande birds are as follows.

31125: Female not breeding. February 26, 1948. Length 132, wing 123, tail 132, extent 308 mm. Black above, sooty brown below; supra-loral spot and small post-ocular patch white; small feathers along edge of wrist and front of wing white-edged; trace of white on chin. Ovary small but distinct.

At 10 P.M. this bird fluttered against a bedroom window. It was later found and captured on the Rancho Grande porch, fluttering confusedly around the electric light. The evening was one of dense fog, with a strong breeze blowing from the southwest.

*Food*: A mass of rather comminuted flying ants. (Weber).
Coleoptera spp.
Hymenoptera: Highly fragmentary *Camponotus* sp., forming most of the contents.

31133: Male, not breeding, April 4, 1948. Length 120, wing 120, tail 39, extent 305 mm. Weight 22.5 grams.

Frontal spots large and pure white, beginning on lores with only a few feathers between them and nostrils, and extending back over eye frame, and on a narrow line to midway over eyes, thus approaching the post-ocular spot. This latter forms the posterior border of the feather circle around the bare area on the lower lid. When the eye is closed and this lid drawn up, the spot is directly behind the eye. When the eye is open it is behind and below eye. Wrist edge of wing and rim featherlets all have distinct white edges. The chin is grayish-white.

The bird was caught at 8:30 P.M. as it clung to the vertical electric light wire depending from the ceiling of the porch outside the laboratory. There was sufficient fog to hide the stars and the recent wind had died down. The air was cool, 62 degrees Fahrenheit, sufficient to keep all moths away.

*Food*: Flying ants. (Weber).
Coleoptera spp.
Hymenoptera: *Camponotus* sp.

*Syrinx*: *C. cherriei*, No. 31133 (KOH No. 2588) differs from *Streptoprocne zonaris albicincta* in there being three, instead of two, rows of post-glottid teeth. The syrinx proper, although completely ossified, shows distinctly its composition of three rings. The median anterior protuberance is directly connected with a slight, posterior, cartilaginous projection of the lowermost free tracheal ring.

31134: Female, not breeding. April 5, 1948. Length 137, wing 127, tail 51, extent 310 mm. Weight 25.5 grams.

Large white preocular spots almost join white chin. Postocular and white wing edges well developed. Flew against laboratory windows at 7:30 P.M. in dense cold fog.

*Food*: Stomach crammed with insects, one-half of which were ants (Weber).
Hemiptera spp.
Coleoptera spp.
Hymenoptera: parasitic sp.
Hymenoptera: *Camponotus* sp. fragmentary.
Hymenoptera: dolichoderine wings.

April 5. At 7:45 two more white-spots came to the porch but both escaped. At 8:10 another bird came and went. In all, the mental white was almost absent.

April 11. In dense, drenching fog a white-spot came to my bedroom window at 9:30 P.M. and clung out of reach to the rough surface of a cement pillar. Eye-white as usual, with more on the chin than in any bird hitherto seen.

May 10. Male bat falcon caught a white-spot, held it for three minutes, with the dangling head in full view. Hardly any mental white, but very large and fluffed out eye spots. After plucking it he gave it to the female who fed her young.

June 13. Female bat falcon brought a swift to her perch, and had begun plucking it when the young male flew up, took it and ate it.

### **Cypseloides cryptus** Zimmer, 1945.

Tropical Black Swift.

*Former Records and Species Range*: In 1945 a new species of swift was described (Zimmer, 1945). The type came from the Rio Tavara, Peru. Only four other specimens were known, taken at the following localities: British Guiana (Kaieteur Falls), Venezuela (Mt. Auyan-tepui, and Saroropan-tepui), and Costa Rica (San Pedro).

Only a single individual of this species was seen at Rancho Grande in 1948. The two which were taken in 1946 have already been reported by me (Beebe, 1947), and I here repeat several paragraphs.

*Field Characters for Sight Identification*: This five-inch black swift would show no definite characters in flight except the general black coloration. The grizzled and variable dull whitish of the lores and chin could hardly be detected.

*Occurrence*: On April 20, 1946, a female of this swift crashed against the laboratory windows at Rancho Grande at 8:30 o'clock in the evening and was stunned. It is No. 30,634, female, not breeding, fairly fat, weight 40.2 grams. Length 120, wing 137, tail 48, extent 355 mm. The stomach was filled with winged female *Azteca* ants.

On April 21, the following evening, at the same time, a second bird killed itself against the identical window. This is No. 30,640, female, not breeding, considerable fat, weight 35.8 grams. Length 138, wing 130, tail 50 mm. First primary in each wing half grown.

*Food*: A great quantity of *Crematogaster* and *Azteca* flying ants.

April 12, 1948. At 10:15 A.M. the male bat falcon swung up to his perch in the top of the candelo tree, with a swift. Through the

20-power glasses I could see every detail and in every respect of the cephalic pale color it seemed to be this species. There was no trace of the supraloral white spots of *cherriei*, and the area around the base of the beak showed the pale grizzled appearance so apparent in both of the specimens taken in 1946. I could have had no more certain evidence if the bird had been in my hand. It was slowly and thoroughly plucked and as the female did not appear, the male proceeded to eat the eighth known individual of *Cypseloides cryptus*.

**Aëronautes montivagus montivagus**
(d'Orbigny and Lafresnaye, 1837).

White-breasted Swift.

*Species and Subspecies Range*: Mountains of northern Venezuela, Peru and Bolivia.

*Field Characters for Sight Identification*: A small five-inch swift. Easily distinguished by great extent of ventral white, no nuchal collar, and almost square tail.

*Occurrence*: Known at Rancho Grande laboratory from a single specimen which flew into the porch in dense neblina, and at about 9:15 P.M. was caught as it crouched in a corner.

31142: Adult male, breeding, testes 8.5 mm. April 23, 1948. Length 120, wing 110, tail 40, extent 266 mm. Weight 20 grams.

*Food*: Many flying ants and small cucurlionid beetles (Weber).

Hymenoptera: ponerine and *Camponotus* ant fragments.

*Parasites*: This swift was strongly infested with parasites, one of which (48375) was a giant feather fly with bright green abdomen. In addition, there were several *Mallophaga*, and a number of bête rouge.

Dr. J. Bequaert has kindly identified the large feather fly, and sends me the following note:

"The fly is *Brachypteromyia neotropica* J. Bequaert. This was described from a single male, taken from the same host species, at Galipan, close to Pico Avila, Estado Mirando, 2,000 meters elevation, Venezuela.[2] Yours is the second specimen known, also a male. The description, with figure, is in Psyche, 49. (1942) published in 1943, p. 113. The only other species of the genus, *Brachypteromyia fimbriata* (Waterhouse), is North American, on the swifts *Aëronautes saxatilis* and *Nephoecetes niger*."

In addition to the single captured specimen of this swift, we have three other records.

June 19, 1948. Six white-breasted swifts flew, one after the other, through the pass at 10 A.M. They were headed south and not flying very fast. While still in sight two of the birds veered aside from their direct flight and caught insects.

June 21, 1948. A compact flock of twelve of these swifts swung south through the pass at 8:05 in the morning. They flew very low, just skimming the trees.

[2] Pico Avila is in the immediate neighborhood of Caracas, about 100 kilometers due east of Rancho Grande.

Three of this species were caught by the male bat falcon; on April 4, June 10 and 19, 1948.

**Panyptila cayennensis** (Gmelin, 1789).

Fork-tailed White-collared Swift.

*Species Range*: Southeastern Nicaragua, south over Colombia, Ecuador, Venezuela, Tobago, Trinidad and the Guianas to Bahia and São Paulo.

*Field Characters for Sight Identification*: A five-inch swift, unmistakably fork-tailed, black except for white eye-spots and flank-spots, chin, throat and collar.

*Occurrence*: 30439: A male flew against the windows of the laboratory and was badly injured. July 1, 1945. Length 123, wing 125, tail 57 mm.

*Food*: Small species of flying ants.

(This specimen was overlooked in the paper on Avian Migration at Rancho Grande, Beebe, 1947).

June 8, 1948. Six fork-tailed swifts hawking about early in the morning with three blue and white swallows, over the compound of Rancho Grande.

June 12, 1948. A swift of this species caught and eaten by male bat falcon.

## Summary.

At Rancho Grande a total of eight species of swifts were collected or observed, out of the thirteen species recorded from Venezuela as a whole. The types of observation resolve into: flocks feeding at various altitudes, others migrating through Portachuelo Pass usually low down, or striking against the lighted windows of the laboratory on nights of fog or rain. Finally a number of the birds were caught by a male bat falcon.

Throughout twenty months of residence during three years no swift was seen to alight, nor was there at Rancho Grande first-hand proof of breeding or roosting colonies, although the latter were indicated as a result of various activities.

Observations in adjoining areas, both higher up the surrounding mountains, and down to four hundred and forty-five meters on the Maracay plain, showed a relative dearth or absence in comparison with their numbers in the square kilometer whose center was Rancho Grande and the pass. The obvious explanation of this concentration of swifts, by day and night, must be the same as that of many other organisms, both vertebrates and invertebrates; viz., the continual procession on migration of countless numbers of insects representative of almost every order, traversing the sixty-foot-wide pass, from north to south, on every clear day throughout the rainy season. This abundant and ever renewed source of food was obviously a focusing factor of prime importance.

A second reason for the abnormal numbers of species and individuals was the use of the pass by several of the species on daily migration from a presumed breeding or roost-

ing place to a trans-pass feeding-area. It is difficult otherwise to account for the forty-four specimens of all eight species taken or observed on black nights of poor visibility. Of twenty-two specimens sexed, seventeen were males, five females.

The presence throughout their breeding season of a pair of bat falcons, close to Rancho Grande, revealed an interesting relationship between these birds and the swifts. The latter showed little fear of the small falcons when these were perched, and giant swifts did not hesitate to attack and drive off the male hawk. Yet I recorded nineteen individuals and seven out of the eight species of swifts as entering into the diet of the hawks. When high in the sky, a power dive attack of the male falcon rendered escape impossible on the part of the swifts, but when the birds met at horizontal levels, the speed and dodging ability of the small birds rendered them safe.

The flocking habits of these Venezuelan swifts are, in some ways, suggestive. Single birds were very rare, and pairs were not often seen. But, especially in mid rainy season months, trios were common. Even in flocks of twenty to fifty, feeding in midair, subdivision into trios was often evident. If the same rule of a single surviving young holds in tropical swifts as in many other tropical birds, these trios probably represented the season's families. Larger flocks in rapid movement were too infrequent to warrant definite classification or object.

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## EXPLANATION OF THE PLATE.

Plate I.

Two migrant swifts which came to the electric lights of Rancho Grande on nights of rain or fog.

Fig. 1. Giant White-collared Swift. *Streptoprocne zonaris albicincta* (Cabanis).

Fig. 2. Chestnut-collared Swift. *Chaeturella rutila brunneitorques* Lafresnaye.

FIG. 1.

FIG. 2.

THE SWIFTS OF RANCHO GRANDE, NORTH-CENTRAL VENEZUELA, WITH SPECIAL REFERENCE TO MIGRATION.

# 9.

# Eastern Pacific Expeditions of the New York Zoological Society. XL. Mollusks from the West Coast of Mexico and Central America. Part VII.[1]

LEO GEORGE HERTLEIN & A. M. STRONG.
*California Academy of Sciences.*

(Plate I).

[This is the fortieth of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

CONTENTS.



## INTRODUCTION.

This is the seventh of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). The general plan of presentation followed in the present contribution is that mentioned in Part II of this series of papers[2]. Formal headings and keys are given for 51 species and subspecies of the Tellinidae collected by the expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated which species do not occur in the present collection.

Acknowledgment is due Dr. G. Dallas Hanna, Curator, Department of Paleontology of the California Academy of Sciences, Mr. A. G. Smith, Research Associate of the same institution, and Dr. A. Myra Keen, Stanford University, California, for assistance and suggestions. Acknowledgment is also due Miss Viola Bristol, Curator of Mollusks, San Diego Society of Natural History, for the loan of specimens. The photographs used for illustrations on the plate were prepared by Mr. Frank L. Rogers.

[1] Contribution No. 842, Department of Tropical Research, New York Zoological Society.

[2] Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXIII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 28, Pt. 3, December 6, 1943, pp. 149-168, pl. 1. See especially pp. 149-150.

## Superfamily Tellinacea.

### Family Tellinidae.

Papers by Dall[3] and Salisbury[4] dealing with the Tellinidae are very useful in a study of West American members of this family.

### Key to the Genera of the Family Tellinidae.

A. Shell with lateral teeth in one or both valves
  a. Exterior with oblique, flexuous, divaricating striae; orbicular ... *Strigilla*
  aa. Exterior usually without, sometimes with, oblique but not flexuous, divaricating striae
    b. Dorsal margins serrate; trigonal; very inequivalve and compressed *Tellidora*
    bb. Dorsal margins not serrate or occasionally so only posteriorly; usually elongate ... *Tellina*
B. Shell without lateral teeth
  a. Suborbicular to subtrigonal; subequilateral; moderately inflated; broad submedian concavity in right valve *Apolymetis*
  aa. Subtrigonal or elongate; posterior end produced and narrowed; moderately compressed; sometimes inequivalve *Macoma*

### Genus *Tellina* Linnaeus.

The present collection from the tropical eastern Pacific contains a good representation of the species of *Tellina* which occur in that region. Many of these shells are conspicuous because of their beautiful red color, especially when observed upon the beach. Mörch long ago mentioned that red Tellinas are characteristic of tropical American waters.

### Key to the Subgenera of *Tellina*.

A. Posterior area with simple concentric lamellae or smooth
  a. Surface obliquely grooved ... *Scissula*
  aa. Surface not obliquely grooved
    b. Beaks anteriorly directed *Macaliopsis*
    bb. Beaks not anteriorly directed
      c. Right anterior lateral distant from the beak
        d. Smooth, polished *Tellina s.s.*[5]
        dd. Strong concentric sculpture *Tellinella*
      cc. Right anterior lateral extends close beneath or near beak
        e. Shell usually exceeding 25 mm. in length
          f. Resilium external; shell elongate
            g. Thick; right posterior lateral strong *Eurytellina*
            gg. Thin; right posterior lateral weak; fine reticulate sculpture *Tellinidella*
          ff. Resilium internal; shell thin, high *Scrobiculina*
        ee. Shell not exceeding 25 mm. in length (usually not exceeding 20 mm.)
          h. Sculpture chiefly of concentric lines of growth (except on posterior area) *Moerella*
          hh. Sculpture chiefly of concentric lamellae (over entire shell); trigonal; strong, very narrow posterior flexure ... *Merisca*
B. Posterior area with plate-like foliations or posterior end with strong radial sculpture
  a. Pallial sinus free or confluent with pallial line for not more than one-third its length
    b. Posterior area with plate-like foliations ... *Phyllodina*
    bb. Posterior end of shell with strong radial sculpture; very small *Elliptotellina*
  aa. Pallial sinus confluent with pallial line for entire length ... *Phyllodella*

### Subgenus *Tellinella* Mörch.

*Tellinella* Gray, Mörch, Cat. Conch. Yoldi, Fasc. 2, 1853, p. 13. [Species originally cited under *Tellinella* include *antoni* Philippi, *interrupta* Solander, *pulchella* Lamarck, *rostrata* Linnaeus, *virgata* Linnaeus, and several others]. —Dall, Bartsch & Rehder, Bernice P. Bishop Mus., *Bull.* 153, July 25, 1938, p. 187. Type: *Tellina virgata* Linnaeus.

*Type* (designated by Stoliczka, *Mem. Geol. Surv. India, Palaeont. Indica*, Ser. 6, Vol. 3, 1870, pp. XVII, 116): *Tellina virgata* Linnaeus [Syst. Nat., ed. 10, 1758, p. 674. "Habitat in O. Indico." Illustrated by Hanley,

[3] Dall, W. H. Synopsis of the Family Tellinidae and of the North American species. *Proc. U. S. Nat. Mus.*, Vol. 23, [No. 1210], November, 1900, pp. 285-326, pls. 2-4.

[4] Salisbury, A. E. On the Nomenclature of Tellinidae, with Descriptions of new species and some remarks on Distribution. *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, pp. 74-91, pls. 9-14.

[5] Not represented in the present collection.

[Thes. Conch., Vol. 1, 1846, p. 228, pl. 63, fig. 212. Indian Ocean].

KEY TO THE SPECIES OF *Tellinella*.

A. Ornamented by radial stripes or spots of chocolate or purple; distance separating pallial sinus from anterior adductor impression 5 mm. or more *cumingii*

B. Ornamented by radial stripes or bands of golden-orange; distance separating pallial sinus from anterior adductor impression not exceeding 2 mm. *zacae*

**Tellina (Tellinella) cumingii** Hanley.

*Tellina cumingii* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 59. "Hab. Guacomayo, Central America; in coral sand." —Hanley, Thes. Conch., Vol. 1, 1847, p. 223, pl. 58, fig. 72. "Guacomayo and America." —M. Smith, Panamic Mar. Shells (Tropical Photogr. Lab., Winter Park, Florida), 1944, p. 64, fig. 847. Lower California to Panama. [Not the record "Red Sea?"].

*Type Locality*: Guacomayo, Central America.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Gorgona Island, Colombia.

*Collecting Stations*: Mexico: Tangola-Tangola Bay (196-D-14, 15), 5 fathoms, crushed shell; Costa Rica: Culebra Bay; Cedro Island (213-D-4), 5 fathoms, mud; off Ballena Bay, Gulf of Nicoya (213-D-15), 40 fathoms, mud.

*Description*: Shell elongate, narrow, rather compressed, subrostrate, somewhat biangulated and bent to the right posteriorly; yellowish-white with radiating brown or chocolate or purplish streaks or spots; sculptured with moderately fine, close, concentric lamellae which become coarser and elevated on the posterior portion of the shell; hinge with two cardinal teeth in each valve, the right posterior and left anterior cardinals grooved, and two equidistant laterals in each valve; pallial sinus rather wide (in young shells rounded but in the adult obliquely pointed at the end), projecting forward about two-thirds the distance between the two adductor impressions and for about two-thirds its length confluent with the pallial line; interior white or pale yellow or a combination of the two.

Large specimens of this species attain a length of 55 mm. or more.

*Tellina interrupta* Wood[6], which ranges from North Carolina to Brazil, is a similar species. *Tellina strophia* Dall, in the Miocene of Florida, also is somewhat similar to *T. cumingii*.

[6] *Tellina interrupta* Wood, General Conch., 1815, p. 146, pl. 36, fig. 3. "Inhabits the Indian and American Seas." Also edit. 1835. [Regarding the dates of issue of this book see Pritchard & Gatliff, *Proc. Roy. Soc. Victoria*, Vol. 16 (N.S.), Pt. 1, September, 1903, p. 114; Iredale, *Proc. Malacol. Soc. London*, Vol. 15, Pts. 2 and 3, December, 1922, p. 91].

Not *Tellina interrupta* Solander, Portland Cat., 1786, pp. 31, 72, 105. *Nomen nudum.*

*Distribution*: A few specimens of this species were taken by the expedition off western Mexico and Costa Rica. The species also is known to occur in the Pleistocene of Magdalena Bay, Lower California.

**Tellina (Tellinella) zacae** Hertlein & Strong, sp. nov.

Plate I, Figs. 12, 13, 17.

Shell of moderate size, elongately ovate, umbos a little posterior to the center, white, with golden-orange radiating bands of varying width; anterior end elliptically rounded, posterior end rather pointed (but acutely rounded at the extremity) and slightly bent toward the right, the ventral margin is broadly curved; right valve with an elevated, rounded, curved ridge radiating from the posterior side of the umbo to the posterior ventral margin and there is a corresponding depression in the left valve; posterior to the ridge the shell is depressed and anterior to the ridge there is a slight sinus; the early part of the shell is ornamented with fine, rounded, concentric threads, these on the adult shell become stronger and slightly irregular and somewhat lamellated posteriorly; ribs separated by interspaces of about the same width or in some instances slightly narrower, very fine concentric threads are present in the interspaces; a short but rather stout ligament on a narrow nymph is present posterior to the umbos; hinge with two cardinals in each valve, the right posterior and the left anterior ones grooved, the other two are more slender, there are two laterals in each valve, those on the right valve are strong, those on the left low and fused with the margin; pallial sinus long, rounded at the end and extending about three-fourths the length of the shell; interior whitish, the external rays showing through the shell. Dimensions of the holotype: length, 33.4 mm.; height, 15.2 mm.; convexity (both valves together), 7.8 mm.; pallial sinus extends anteriorly 25 mm. from the posterior end of the shell.

Holotype (California Acad. Sci. Paleo. Type Coll.), from Station 136-D-1, Arena Bank in the Gulf of California, Lat. 23° 29′ N., Long. 109° 25′ W., dredged in 45 fathoms (82 meters), mud. Paratypes were dredged in the same general region at Station 136-D-31-32, Lat. 23° 24′ 30″ to 23° 28′ N., Long. 109° 24′ to 109° 23′ 30″ W., in 35-42 fathoms, in sand, calcareous algae and weeds. Other specimens were dredged at Station 150-D-12, Gorda Banks in the Gulf of California, Lat. 23° 02′ N., Long. 109° 28′ W., in 80-90 fathoms, sand.

The shell of this new species is in general features similar to that of *Tellina cumingii* but it differs in several details. In the present species the posterior area on the left valve possesses a deep well-developed groove corresponding to a ridge in the opposite valve, while in *T. cumingii* the corresponding area on the left valve is somewhat flat-

tened and dorsally bounded by a fine incised radial line. The pallial sinus of the new species is more evenly rounded at the anterior end and extends much nearer (about three-fourths the length of the shell) the anterior adductor impression than that of *T. cumingii*. Furthermore in the color pattern the beautiful radial orange stripes on a white ground attain greater width than the purple stripes which occur on a yellowish-white ground on *T. cumingii*. The specimens of the new species in the present collection do not attain the size of *Tellina cumingii*.

*Tellina zacae* bears a resemblance to *Tellina crassiplicata* Sowerby as illustrated by Dall, Bartsch & Rehder[7] from Hawaii, but is narrower anteriorly and less broadly truncated posteriorly. The original illustration of *Tellina crassiplicata*[8] does not show any radial stripes.

### Subgenus **Scrobiculina** Dall.

*Scrobiculina* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 290. "Type, *Scrobicularia viridotincta* Carpenter."

*Schumacheria* Cossman, *Rev. Crit. de Paléozool.*, Vol. 6, No. 1, January, 1902, p. 52. New name for *Scrobiculina* Dall, not *Scrobiculinus* Monterosato, 1884.

*Type* (by original designation): *Scrobicularia viridotinca* Carpenter.

Cossman proposed the name *Schumacheria* to replace *Scrobiculina* Dall, 1900, because of the prior name *Scrobiculinus* Monterosato, 1884.

A strict interpretation of the present International Rules of Zoological Nomenclature (Article 36), allows the retention of *Scrobiculina* Dall.

### Key to the species of *Scrobiculina*.

A. Color of umbos ochraceous ..... *ochracea*
B. Color of umbos yellowish-green *viridotincta*

#### **Tellina (Scrobiculina) ochracea** Carpenter.

*Tellina* (*Peronaeoderma*) *ochracea* Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 13, April, 1864, p. 312. Cape St. Lucas. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 210.

*Tellina* (*Scrobiculina*) *ochracea* Carpenter, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302. "Cape St. Lucas to the Gulf of California."

*Type Locality*: Cape San Lucas, Lower California.

*Range*: Cape San Lucas to the Gulf of California.

*Collecting Station*: Mexico: Arena Bank, Gulf of California (136-D-6), 45 fathoms mud, *Arca* conglomerate.

*Description*: Two somewhat worn and broken specimens in the present collection answer to the description of *Tellina ochracea*. They are colored a light sulphurous yellow strongest near the beaks and fading gradually toward the margins. Dall (1900), stated that the species was very similar to *Tellina viridotincta* Carpenter, differing only in color. From the ranges given by Dall it would seem that *Tellina viridotincta* is a more southern shell while *T. ochracea* is a species of the Gulf of California. The green tip of the beak of *T. viridotincta* may not be a constant character because Stearns and Pilsbry & Lowe have recorded it well within the range of *T. ochracea*. If the color differences do not prove to be constant, *viridotincta*, being the older name, should take precedence.

*Distribution*: A few specimens referred to this species were dredged by the expedition on Arena Bank in the Gulf of California in 45 fathoms.

#### **Tellina (Scrobiculina) viridotincta** Carpenter.

*?Scrobicularia virido-tincta* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 160. "Hab. in Sinu Panamensi, una cum. *?S. producta;* legit T. Bridges. Sp. un. in Mus. Cuming."

*Macoma viriditincta* Carpenter, Stearns, *Proc. U. S. Nat. Mus.*, Vol. 17, 1894, p. 156. La Paz; various localities in the Gulf of California.

*Tellina* (*Scrobiculina*) *viridotincta* Carpenter, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302. Lower California to Panama.

*Tellina viridotincta* Carpenter, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 133. Espiritu Santo Island; La Paz.

*Type Locality*: Bay of Panama.

*Range*: Gulf of California to Panama.

*Collecting Station*: Mexico: Port Guatulco (195-D-6), 3 fathoms, sand, algae, crushed shell.

*Description*: Shell large, high, oval, beaks posterior to the center, anterior end elliptically rounded, ventral margin broadly rounded, posterior end tapering, subtruncately rounded and bluntly pointed at the extremity; white, umbos greenish-yellow; posterior area set off by a low umbonal ridge and anterior to this there is a low, broad, radial depression; valves ornamented with fine, rather regular, concentric threads and striae, which are more crowded and irregular on the posterior area on which, especially on the right valve, there is usually one and sometimes more fine radial ridges; the concentric sculpture is crossed by very fine, faint, radiating striae over much of the disk; the pallial sinus extends about three-fourths the length of the shell, highest somewhat anterior to the posterior adductor impression then sloping downward anteriorly where, at about 5-8 mm. from the pallial line, it is sub-

[7] *Tellina crassiplicata* Sowerby, Dall, Bartsch & Rehder, Bernice P. Bishop Mus., *Bull. 153*, July 25, 1938, p. 187, pl. 48, figs. 5-8. Various localities in Hawaii cited, also Midway Island and Ocean Island.

[8] *Tellina crassiplicata* Sowerby, Conch. Icon., Vol. 17, *Tellina*, April, 1869, species 332, pl. 56, figs. 332a, 332b. "Hab. Sandwich Islands."

ngularly or bluntly rounded and then joins he pallial line; a large sunken ligament is ituated upon a nymph; hinge with two carinals in each valve, the right posterior and eft anterior ones grooved; right valve with wo well-developed laterals, left valve with weak anterior lateral and the posterior ateral very slight or obsolete; interior white vith blotches of greenish-yellow, especially oward the dorsal portion of the shell.

A specimen from the Gulf of California n the Henry Hemphill collection of the California Academy of Sciences, measures: ength, 62 mm.; height, 44 mm.; convexity (both valves together), 14.5 mm.; pallial sinus extends anteriorly 46 mm. from the posterior end of the shell. The species attains a greater size than this.

As mentioned by Dall, about the only difference between *Tellina viridotincta* and *T. ochracea* is in color.

*Distribution*: One rather worn pair of valves of this species was dredged in 3 fathoms at Port Guatulco, Mexico.

Subgenus **Moerella** Fischer.

*Moerella* Fischer, Man. de Conchyl., Fasc. 11, June 15, 1887, p. 1147. Sole species, *Tellina donacina* Linnaeus.

*Type* (by monotypy): *Tellina donacina* Linnaeus. Recent, seas of Europe. Illustrated by Bucquoy, Dautzenberg & Dollfus, Moll. Mar. Roussillon, Vol. 2, Fasc. 25, March, 1898, p. 648, pl. 91, figs. 13, 14, and vars. 15-19. Mediterranean. Also other localities cited.

In the present paper nine species and subspecies have been referred to the subgenus *Moerella*. Some of these, in earlier publications, have been referred to *Angulus* Megerle von Mühlfeld. The type of *Angulus* designated by Gray, 1847, is *Tellina lanceolata* Linnaeus, a species in which the hinge is said to possess a right anterior lateral but lacking all other laterals. Salisbury, 1934, stated that only two Recent species, *T. lanceolata*, the type, and *T. armata* Sowerby, were referable to *Angulus*. However, in the explanation to his plates five species are referred to *Angulus*. It is unfortunate that this well known supraspecific group name should be applicable to so few species.

All the species in the present paper which have been referred to *Moerella*, although varying somewhat in shape, possess a right posterior lateral tooth of varying strength. This lateral occurs just below a socket which is present just below the ventral end of the nymph upon which the ligament is situated.

The results of our studies which have led us to place the following group of species under the subgenus *Moerella*, are in agreement with the conclusions reached by Gardner[9] with regard to the east American Miocene and Pliocene species formerly referred to *Angulus*.

[9] Gardner, J., *U. S. Geol. Surv., Prof. Paper 142-E*, 1928, p. 195; *U. S. Geol. Surv., Prof. Paper 199-A*, 1943, p. 94.

KEY TO THE SPECIES OF *Moerella*.

A. Posterior end triangular or bluntly pointed
  a. Posterior end the longer, tapering, pointed; white, yellowish or pinkish ..... *suffusa*
  aa. Anterior end the longer
    b. Posterior dorsal margin sinuous; ivory white ..... *tabogensis*
    bb. Posterior dorsal margin straight or slightly curved
      c. Ventral margin strongly curved; posterior end blunt; white ..... *paziana*
      cc. Ventral margin very gently curved
        d. Length more than twice the height; white, occasionally yellowish ..... *amianta*
        dd. Length less than twice the height
          e. Area anterior to posterior umbonal angulation strongly depressed; usually pink on dorsal margins ..... *erythronotus*
          ee. Area anterior to posterior umbonal angulation not depressed or only faintly so; red or pink zoned with white
            f. Umbos moderately inflated; posterior end very short ..... *macneilii*
            ff. Umbos rather compressed; posterior end more attenuated; rose red ..... *felix*
B. Posterior end broad, obliquely truncated
  a. Pale rose color ..... *arenica*
  aa. White; posterior end more abruptly truncated ..... *recurvata*

**Tellina (Moerella) amianta** Dall.

*Tellina* (*Moerella*) *amianta* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 317, pl. 3, fig. 12. "Dredged in 14 fathoms, sand, off Cape Tepoca, Lower California, near the head of the Gulf, by the U. S. Fish Commission at station 3019."

*Type Locality*: Off Cape Tepoca, Lower California, near the head of the Gulf of California, in 14 fathoms, sand.

*Range*: Gulf of California to Colombia.

*Collecting Station*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves, sand, also on shore in beach drift; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, shelly mud, crushed shell.

*Description*: Shell small, elongated, anteriorly produced and rounded, the posterior end shorter, obliquely truncated and rather

pointed at the extremity; sculptured with fine, close, concentric threads which toward the posterior angulation become somewhat irregular, sharper, and in the adult shell two or three ribs coalesce to form low raised lamellae on the posterior area; hinge with two cardinals in each valve, the right posterior and left anterior ones grooved, right valve with a strong fairly close anterior lateral and a small posterior lateral; pallial sinus extends near to, but does not touch, the anterior adductor impression, confluent with the pallial line below; color white or partly salmon yellow.

A large right valve dredged in Santa Inez Bay in the Gulf of California in 4-13 fathoms, measures: length, 14 mm.; height, 6.8 mm.; convexity (one valve), 2.2 mm.

The small size, elongate form which is much produced anteriorly, and fine, close, concentric sculpture are characteristic features of this species.

Specimens dredged by the expedition in Santa Inez Bay in the Gulf of California are typical of the species. Specimens collected at Corinto, Nicaragua, in beach drift, and dredged in 12-13 fathoms agree in general characters with *T. amianta* except that they are thinner. Many small specimens dredged in 12-13 fathoms off Port Parker, Costa Rica, in which the hinge, concentric sculpture and other general characters agree well with *T. amianta,* appear to represent the young of that species. Some are less elongate in proportion to the height as compared to typical *T. amianta* but this appears to be somewhat variable among these young shells.

Many small specimens in the collections of the California Academy of Sciences, dredged in the Gulf of California, are similar to *T. amianta.* Some are white, some white with pink radial streaks or dots, others yellowish-white. These bear a similarity to one of the illustrations given by Sowerby[10] (pl. 47, fig. 278d) under the name of *Tellina silicula* Deshayes. That species was originally described by Deshayes[11] with the type locality "W. Columbia." Salisbury[12] stated that the type specimen of *T. silicula* Deshayes is referable to *Tellina rhomboides* Quoy & Gaimard, a species which occurs in the western Pacific region. According to Iredale[13] *Tellina clathrata* Deshayes is the correct name for that species. Sowerby's figures 278a, b, c, appear to be referable to it but it seems possible that his figure 278d might be referable to a young *T. amianta.*

*Distribution*: This species was dredged in Santa Inez Bay, Gulf of California, in 4-13 fathoms, at Corinto, Nicaragua, in 12-13 fathoms, also in beach drift on shore, and a Port Parker, Costa Rica, in 12-15 fathoms It also has been recorded as occurring in th Pleistocene at Magdalena Bay, Lower Cali fornia.

**Tellina (Moerella) arenica** Hertlein & Strong sp. nov.

Plate I, Figs. 5, 11.

*Tellina carpenteri* Dall, Packard, *Univ Calif. Publ. Zool.*, Vol. 14, No. 2, Septembe 12, 1918, p. 276, pl. 25, figs. 10a, 10b. . . "in 68 fathoms just south of the Farallo Islands." —I. S. Oldroyd, *Publ. Puget Sound Biol. Sta.*, Vol. 4, 1924, pl. 41, figs. 10a, 10b (Copies of Packard's figures). —I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol Sci.*, Vol. 1, 1924, pl. 44, figs. 10a, 10b (Copies of Packard's figures).

Not *Tellina carpenteri* Dall, 1903.

*Description*: Shell of moderate size, transversely ovate, thin, compressed, the anterio end slightly the longer, color creamy white salmon pink and rose in concentric zones of irregular width; anterior dorsal margin sloping gently convexly from the beaks, anterior end rounded, ventral margin broadly rounded, posterior dorsal margin gently sloping, slightly concave, posterior end obliquely truncated; posterior area defined only by a rounded umbonal angulation; sculptured with concentric lines of growth and by somewhat irregularly spaced fine, shallow, concentric grooves which on the posterior area become deeper and give rise to sublamellate sculpture; hinge of right valve with two cardinal teeth, the posterior one bifid, an anterior lateral is fairly close to the cardinals and there is a distant posterior lateral below a socket; left valve (paratype) with a bifid anterior cardinal and traces of a posterior cardinal (some valves with a thin posterior cardinal lamella); pallial sinus highly trigonal back of the beak then sloping somewhat irregularly to a position below and well separated from the anterior adductor impression, the end rounded then bending posteriorly for a very short distance where it becomes confluent with the pallial line; interior white and pink. Dimensions of the holotype: length, 24.5 mm.; height, 15 mm.; convexity (one valve), 2.5 mm.; pallial sinus extends anteriorly 19 mm. from the posterior end of the valve.

Holotype, a right valve (Calif. Acad. Sci. Paleo. Type Coll.), dredged at Station 136-D-20 in Lat. 23° 30′ N., Long. 109° 26′ W., in 43 fathoms, mud, on Arena Bank, at the south end of the Gulf of California. One additional specimen, a paratype, was dredged at the same locality. Three small single valves were dredged in the channel east of Cedros Island at Station 126-D-17, in 40 fathoms. Paratypes were dredged by the Templeton Crocker Expedition in 1932, near Puntarenas, Costa Rica.

*Range*: Farallon Islands, California, to Panama.

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[10] Sowerby, G. B., Conch. Icon., Vol. 17, *Tellina*, October, 1868, species 278, pl. 47, fig. 278d. "Hab. W. Columbia." [Not figs. 278a, b, c.].

[11] *Tellina silicula* Desbayes, *Proc. Zool. Soc. London* for 1854, (issued May 16, 1855), p. 363. "Hab. Columbia. Coll. Cuming."

[12] Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 89. See also Lamy, E., *Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 24, No. 2, 1918, p. 116.

[13] Iredale, T., *Mem. Queensland Mus.*, Vol. 9, Pt. 3, June 29, 1929, p. 266.

This beautiful species has often been referred to *Tellina carpenteri* Dall[14], a distinct species, which has a smaller shell and a generally more northern distribution. Dall[15] cited *T. carpenteri* as occurring in the Gulf of Panama at a depth of 182 fathoms. It seems probable that that record may be referable to the present species.

The form illustrated under the name of *T. carpenteri* by Packard, 1918, which was dredged in 68 fathoms just south of the Farallon Islands, the illustrations of which were reproduced by I. S. Oldroyd, appears to be identical with the present specimens. This new species differs from *T. carpenteri* in the much greater size, irregular concentric zones of color and in the stronger concentric grooves. It differs from *Tellina recurvata* Hertlein & Strong [=*T. recurva* Dall, 1900, not of Deshayes, 1844], in the much more obliquely truncated posterior end and in the pink coloration. The shell of *Tellina arenica* differs from that of *T. tabogensis* in the larger size, pink color and in that the posterior dorsal margin is slightly concave or nearly straight rather than flexuous.

**Tellina (Moerella) erythronotus** Pilsbry & Lowe.

*Tellina* (*Angulus*) *erythronotus* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 94, pl. 12, fig. 7. "Panama, east of the city" (type). Also from Montijo Bay, Panama.

*Type Locality*: Panama, east of the city.

*Range*: Magdalena Bay, Lower California, to the Bay of Panama.

*Collecting Stations*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-8-16, 19-25), 3-16 fathoms, mud, mangrove leaves; Nicaragua: Monypenny Point, Gulf of Fonseca (199-D-2-6), 4-7 fathoms, mud.

*Description*: Shell donaciform, moderately thin, somewhat compressed, creamy white often tinged with pink around the margins, opalescent; anteriorly elongated and rounded, ventrally gently rounded and posteriorly slightly embayed due to the presence of a shallow depressed area which occurs anterior to the posterior umbonal ridge; posteriorly triangular and somewhat bluntly pointed, with nearly straight dorsal margin; pallial sinus long not quite touching the anterior adductor impression, along the base wholly confluent with the pallial line; hinge of right valve with a grooved anterior and a bifid posterior cardinal, the anterior lateral strong and close to the cardinals, the posterior lateral farther removed but not distant; left valve with a grooved anterior and a thin posterior cardinal lamina, anterior lateral represented by a triangular projection of the margin, a similar posterior projection faintly developed or absent.

One of the largest specimens in the present collection measures: length, 25 mm.; height, 14.5 mm.; convexity (both valves together), 7 mm.

The specimens in the present collection show all the characters of *Tellina erythronotus* mentioned by Pilsbry & Lowe.

The shell of this species appears to be very similar to that of *Tellina hiberna* Hanley[16] which also has been cited as occurring at Panama. However, the shell of *T. erythronotus* appears to be somewhat more elongate in comparison to the figures of *T. hiberna* given by Hanley and Salisbury. The posterior dorsal margin of Hanley's species is said to be first convex then concave, but there is no marked convexity on the margin of *T. erythronotus*. Furthermore there is nothing in Hanley's description regarding pink or prismatic colors such as often can be observed on *T. erythronotus*.

*Tellina puellula* Salisbury[17] (=*T. puella* C. B. Adams, not Hanley), is another closely related species. According to Pilsbry & Lowe it is larger, relatively higher and thicker than *T. erythronotus*.

*Tellina hiberna* was described in 1844 and it seems possible that either *T. erythronotus* or *T. puellula*, both described later, may be referable to it, but we have not the type specimens available to enable us to make any definite decision on this question.

*Tellina panamensis* Philippi[18], from Panama, was described as white with the umbos red both exteriorly and interiorly but it was said to lack lateral teeth.

*Distribution*: *Tellina erythronotus* was dredged quite abundantly in the Gulf of Fonseca at a depth of 3 to 16 fathoms on a bottom of mud and mangrove leaves. The present

[14] *Angulus variegatus* Carpenter, *Rept. Brit. Assoc. Adv. Sci.* for 1863 (issued August, 1864), p. 611. "Mont., Cat. Is., 20-60 fm.; rare (Neeah Bay, Swan)." Also pp. 627, 639. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 97, 113. 125. —Carpenter, *Ann. & Mag. Nat. Hist.*, Ser. 3, Vol. 14, December,1864, p. 423. "Hab. Neeah Bay (Swan); Monterey and Catalina Island, 20-60 fathoms, rare (Cooper)." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 235.

Not *Tellina variegata* Gmelin, Syst. Nat., ed. 13, 1790, p. 3237.

*Tellina* (*Angulus*) *carpenteri* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1903, pp. 303, 320. New name for *Angulus variegatus* Carpenter, 1864, not *Tellina variegata* Gmelin, 1790. "Strait of Juan de Fuca to Lower California." Illustrated by I. S. Oldroyd, *Publ. Puget Sound Biol. Sta.*, Vol. 4, 1924, p. 51, pl. 10, fig. 4. —I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 166, pl. 29, fig. 2. San Pedro, California.

[15] *Tellina* (*Angulus*) *carpenteri* Dall, Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 421. "U. S. S. 'Albatross', station 3355, Gulf of Panama, in 182 fathoms, mud, bottom temperature, 54°.1 F. U. S. N. Mus. 122. 934."

[16] *Tellina hiberna* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 148. "Hab. Panama and Bay of Quayaquil; six to eleven fathoms, in sandy mud: Cuming." —Hanley, Thes. Conch., Vol. 1, 1846, p. 282, pl. 57, fig. 53. Original localities cited.

*Tellina* (*Angulus*) *hiberna* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 13, figs. 7, 8, 9. [Illustrations of holotype and paratypes].

[17] *Tellina puellula* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. A new name for *Tellina puella* C. B. Adams, *Ann. & Lyceum Nat. Hist. New York*, Vol. 5, July 1852, pp. 507, 546 (separate, pp. 283, 322). "Panama." Not *Tellina puella* Hanley, *Proc. Zool. Soc. London*, February, 1845, p. 165. "Hab. Senegal. Cuming. Metcalfe."

[18] *Tellina panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 11, 1848, p. 175. "Ad Panama legit frater E. B. Philippi."

records of occurence furnish a long extension north of the known range of the species. The northernmost occurrence of this species known to us is that based upon a specimen in the collections of the California Academy of Sciences which was collected by C. R. Orcutt at Magdalena Bay, Lower California.

### *Tellina (Moerella) felix* Hanley.

Plate I, Fig. 1.

*Tellina felix* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 71. "Hab. Panama; sandy mud, six to ten fathoms." – Hanley, Thes. Conch., Vol. 1, 1846, p. 281, pl. 57, fig. 52. "Panama."

*Type Locality*: Panama, in 6 to 10 fathoms, sandy mud.

*Range*: Mazatlan, Mexico, to Zorritos, Peru.

*Collecting Station*: Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Corinto (200-D-8, 9, 17, 19), 6-13 fathoms, sand, mangrove leaves, also beach drift.

*Description*: Shell small, elongate, anterior end much the longer, rounded, the posterior end very short and obtusely obliquely subtruncated, anterior dorsal and ventral margins nearly parallel, exterior and interior of a glossy rose red color; a posterior area is set off by an umbonal angulation; valves ornamented with fine, regular, concentric striae; hinge of right valve with two cardinals, the posterior one grooved, a strong, high, elongate anterior lateral extends almost to the beak and a small posterior lateral is present just beyond and below the posterior end of the ligamentary area; left valve with a well-developed anterior cardinal, a thin posterior cardinal lamella is almost fused to the posterior margin and a pointed projection of the nymph represents an anterior lateral; pallial sinus not quite reaching the anterior adductor impression and along the base, except for a short distance, it is confluent with the pallial line.

A specimen from the Gulf of Fonseca in the Henry Hemphill collection in the California Academy of Sciences measures approximately: length 17.2 mm.; height, 9.4 mm.; convexity (both valves together), 4.3 mm.

The shell of this little species is characterized by the beautiful glossy rose red color, weakly inflated valves, nearly parallel anterior dorsal and ventral margins, strong right anterior lateral, and by the short, obliquely subtruncated posterior end.

The shorter posterior end, more gently sloping anterior dorsal margin and deep red color are features which serve to separate *Tellina felix* from *T. tabogensis* Salisbury.

The longer, stronger, right anterior lateral and more steeply sloping posterior dorsal area just below the beaks are features separating *T. felix* from *T. carpenteri* Dall.

Carpenter[19] mentioned that *Tellina puella* C. B. Adams[20] [=*T. puellula* Salisbury] is "not unlike *T. felix*." The remarks of Pilsbry & Lowe seem to indicate that the species described by Adams possesses a higher, heavier shell than *T. felix*.

*Distribution*: Specimens of this species were dredged off Nicaragua in 6-13 fathoms and also were taken in the beach drift. It has been recorded with doubt, as occurring in the Miocene[21] of Peru, and definitely in the Pliocene of Ecuador. This species has been cited as occuring in the Red Sea but, as mentioned by Lamy[22], it does not occur in that region.

### *Tellina (Moerella) macneilii* Dall.

*Tellina (Angulus) macneilii* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 318, pl. 3, fig. 7. "Obtained at Guaymas, Mexico, by W. H. Dall."

*Type Locality*: Guaymas, Mexico.

*Range*: Guaymas, Mexico, to the Gulf of Nicoya, Costa Rica.

*Collecting Station*: Costa Rica: Cedro Island to off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell small, solid, inequilateral, the anterior end longer, rounded, the posterior end quite short, depressed, bluntly pointed; color deep rosy, slightly zoned, and paler toward the basal margin; surface closely, sharply concentrically striated, the posterior dorsal area feebly imbricate, with a little obscure radial striulation; valves moderately full, flattish toward the middle of the disk; hinge strong, normal; internal ray obscure; pallial sinus long, nearly reaching the anterior adductor scar, wholly confluent below. Lon. 12.5, alt. 7.6, diam. 3.5 mm. (Original description).

One pair and two single valves dredged in the Gulf of Nicoya agree well with Dall's description and illustration. The largest specimen measures approximately: length 11.5 mm.; height, 7.3 mm.; convexity (both valves together), 4.2 mm. These are identical with specimens identified as *T. macneilii* in the Lowe collection in the San Diego Society of Natural History.

The hinge of this species is similar to that of *T. felix* Hanley.

Compared to *T. felix*, the valves of *T. macneilii* are more inflated in proportion to their size, less elongate, the posterior end is more abruptly truncated and the anterior dorsal margin slopes more steeply. These same characters (except the slope of the anterior dorsal margin) as well as the pink color likewise serve to separate this species from *T. tabogensis*.

*Tellina guaymasensis* Pilsbry & Lowe[23] is

[19] Carpenter, P. P., *Proc. Zool. Soc. London*, 1863, p. 366. Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, p. 202.

[20] See footnote No. 17, p. 69.

[21] *Tellina (Eurytellina)* cf. *felix* Hanley, Olsson, *Bull. Amer. Paleo.*, Vol. 19, No. 68, June 30, 1932, p. 123, pl. 14, fig. 8. "Tumbez formation, Que Tucillal at Zorritos." Peru. Miocene.

[22] Lamy, E., *Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 24, No. 2, 1918, p. 119 (footnote).

[23] *Tellina (Angulus) guaymasensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 94, pl. 16, fig. 7. "Guaymas." Mexico.

quite similar to *T. macneilii* but the shell appears to be a little more depressed medially and is in greater part white with streaks of pink.

The present specimens agree well with the brief description of *Tellina deshayesii* Carpenter[24] from the Bay of Panama. It was said to resemble *Tellina similis* Sowerby but much more inequilateral. However the specific name proposed by Carpenter is untenable in any case because of the prior use of that combination of names, *Tellina deshayesii*, by Hanley[25].

*Distribution*: Specimens of *Tellina macneilii* were taken by the expedition in the Gulf of Nicoya in 35-40 fathoms. This record represents an extension south of the known range of this species.

### *Tellina (Moerella) paziana* Dall.

*Tellina (Moerella) paziana* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 318, pl. 3, fig. 8. "Dredged in 26½ fathoms, near La Paz, Lower California, by the U. S. Fish Commission, at station 2823."

*Type Locality*: Near La Paz, Lower California, Mexico, in 26½ fathoms.

*Range*: Gulf of California to Cedro Island, Costa Rica.

*Collecting Stations*: Mexico: Port Guatulco (195-D-2, 7, 10, 11), 3-5 fathoms, sand, gr. sand, crushed shell, dead coral; Tangola-Tangola Bay (196-D-6, 7, 13, 14, 15), 5-12.8 fathoms, sand, crushed shell; Nicaragua: Corinto (200-D-8, 9, 19,), 6-13 fathoms, mangrove leaves, also on the beach; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell.

*Description*: Shell small, thin, white, convex, the anterior end slightly longer, rounded, the posterior end bluntly pointed; surface finely concentrically sculptured by the incremental lines, covered with a very delicate dehiscent pale straw-colored epidermis; hinge well-developed, a minute but distinct anterior left lateral present; interior polished, only about half the lower portion of the pallial sinus confluent, the anterior part not reaching the adductor. Lon. 10.2, alt. 7, diam. 3.5 mm. (Original description).

The shell of this species is usually small, about 10-15 mm. in length. A large right valve in the present collection from Corinto, Nicaragua, measures approximately: length, 17.5 mm.; height 14 mm., convexity (one valve), 3.3 mm.; pallial sinus extends forward 12.8 mm. from the posterior margin.

The pallial sinus in this species ascends to a high rounded point slightly posterior to a line vertical with the beaks, then descends obliquely. The end is rounded and well separated from the anterior adductor impression.

*Tellina paziana* somewhat resembles *T. meropsis* Dall. It differs from that species in the more elongate outline, the anterior end is longer in proportion to the length, the posterior end is much more bluntly pointed and the pallial sinus is separated from the anterior adductor impression by a much wider space. According to Dall, "This differs from the young of *Scrobiculina viridotincta* Carpenter, which in outline it resembles, by being less polished, more inflated, and without the deep-set resilium."

*Distribution*: This species was taken by the expedition from off western Mexico to the Gulf of Nicoya, Costa Rica, in 3-13 fathoms, also on the beach. This is an extension south of the known range of this species.

### *Tellina (Moerella) recurvata* Hertlein & Strong, sp. nov.

Plate I, Figs. 2, 3, 4, 8.

*Tellina (Angulus) recurva* Dall, *Proc.* U. *S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 304, 320, pl. 3, fig. 4. "Dredged near the head of the Gulf of California in 24 fathoms, mud, off Point Fermin."

Not *Tellina recurva* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 361. "Hab. Australia."—Hedley, *Proc. Linn. Soc. New South Wales*, Vol. 38, Pt. 2, 1913, p. 272. Hedley stated: "I failed to find this unfigured Australian species in the British Museum. It is recommeded that the name be treated as lost and unrecognizable."

*Description*: Shell small, translucent white, polished, rather compressed, beaks very low, the anterior end the longer; anterior dorsal margin gently curved, ventral margin gently rounded, posterior dorsal margin depressed below the beak, sloping gently along the ligamentary area (about 2 mm. on the type), the end obliquely sloping and roundly truncated; a weak posterior umbonal angulation present; surface of valves with concentric, chiefly incremental sculpture, the posterior area with low lamellae; hinge plate arched anterior to the beaks; right valve with two cardinals, the posterior one grooved, anterior lateral strong and fairly close to the cardinals, a posterior lateral occurs below a socket at about the end of the ligamental area; left valve with two cardinals, the posterior one sloping posteriorly, a faint projection of the margin represents an anterior lateral; pallial sinus subtriangular, extending forward about three-fourths the length of the shell but well separated from the anterior adductor impression, along the base confluent with the pallial line. Dimensions of the type: length, 12 mm.; height, 7.5 mm.; convexity (both valves together), 2.9 mm.

Holotype (Calif. Acad. Sci. Paleo. Type Coll.), from Loc. 23802 (C.A.S.), San Luis Gonzaga Bay, Gulf of California. Paratypes from the same locality. Dredged by the expedition at the following stations: Mexico: 4 miles SSW. of Maldanado Point (192-D-

[24] *Tellina deshayesii* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 160. "Hab. in Sinu Panamensi; legit T. Bridges. Sp. un. in Mus. Cuming."

[25] *Tellina deshayesii* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 148. "Hab. Red Sea? Mus. Cuming, Deshayes."

1), 26 fathoms, mud; Port Guatulco (195-D-20), 23 fathoms, mud; Costa Rica: Port Parker (203-D-1), 15 fathoms, sandy mud, crushed shell.

*Range*: Point Firmin, Lower California, near the head of the Gulf of California, to Port Parker, Costa Rica.

Some of the shells of this species are iridescent. Dall pointed out that the shell of this species somewhat resembles that of young *Macoma yoldiformis* but is more blunt posteriorly and the hinge of course is different. The more abruptly truncated posterior end and white color are features separating the present species from *T. arenica*. Compared to *T. tabogensis* the outline of *T. recurvata* is less elongate, the anterior dorsal margin is more arcuate and the posterior dorsal margin is not flexuous. Compared to *T. buttoni* Dall, the shell of the present species is less attenuated both anteriorly and posteriorly, the posterior dorsal margin just below the beaks slopes more gently and it lacks the strong anterior ray internally which is so conspicuous in Dall's species.

*Distribution*: A few specimens of this species were dredged by the expedition off western Mexico in 23-26 fathoms and off Port Parker, Costa Rica, in 15 fathoms. The present record of the occurrence of this shell off Costa Rica is an extension south of the known range of the species.

**Tellina (Moerella) suffusa** Dall.

*Tellina* (*Angulus*) *suffusa* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 303, 319, pl. 3, fig. 10. "Collected at San Ignacio Lagoon, Lower California, by Henry Hemphill."

*Type Locality*: San Ignacio Lagoon, west coast of Lower California.

*Range*: San Ignacio Lagoon, Lower California, to Corinto, Nicaragua.

*Collecting Station*: Nicaragua: Corinto, beach.

*Description*: Shell cuneate, very thin, convex, blunt in front, pointed behind, the posterior end slightly longer, pinkish, yellowish, or translucent white in color; surface rather strongly, closely, and irregularly concentrically striate, with an unusually large and wide lunular impression, but no escutcheon to speak of; hinge normal, delicate; interior polished; the pallial sinus high, well separated from the anterior adductor, though there seems to be no trace of a ray in the specimens examined. Lon. 13.5, alt. 9.2, diam. 4.7 mm. (Original description).

The unusually large lunular area, short, blunt anterior end and pointed posterior end are features characteristic of this little species.

Several single valves from Corinto, Nicaragua, the largest measuring 11 mm. in length, agree well with Dall's description and illustration of *Tellina suffusa*. They likewise appear to be identical with specimens of that species from Magdalena Bay in the Hemphill collection of the California Academy of Sciences.

*Tellina pumila* Hanley,[26] described from Chile, is somewhat similar in outline but the posterior end is narrower.

*Distribution*: Specimens of this species were taken by the expedition only in beach drift at Corinto, Nicaragua. This is a considerable extension south of the known range of this species.

**Tellina (Moerella) tabogensis** Salisbury.

*Tellina* (*Angulus*) *panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 319, pl. 3, fig. 3. "Types.—No. 108557, U.S.N.M., dredged in 30 fathoms in Panama Bay by the U. S. Fish Commission, at station 2799."

Not *Tellina panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 11, 1848, p. 175. "Ad Panama legit frater E. B. Philippi."

*Tellina tabogensis* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. A new name for *Tellina* (*Angulus*) *panamensis* Dall, 1900, not *Tellina panamensis* Philippi, 1848.

*Type Locality*: Panama Bay, in 30 fathoms.

*Range*: Gulf of California to Santa Elena Bay, Ecuador.

*Collecting Stations*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union (199-D-13), 6 fathoms, mud; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1-10), 4-10 fathoms, mud, sand, crushed shell.

Shell small, thin, ivory white, polished, rather compressed, flexuous behind, the anterior end much the longer, produced and rounded, posterior end with the ligament rather deeply inset, margin obliquely descending to a rather blunt point; surface smooth or marked only by incremental lines, except near the basal margin, where there are a few incised lines with wider interspaces, not quite in harmony with the lines of growth; posterior dorsal area minutely concentrically rippled; hinge normal, delicate; pallial sinus large, not reaching the adductor, mostly confluent below; the elevated ray absent or obsolete. Lon. 9, alt. 5.25, diam. 2.5 mm. (Original description of *Tellina panamensis* Dall).

Fresh specimens exhibit on the surface a lovely iridescent glow (Dall).

A large series of specimens of this species dredged off El Salvador by the expedition have been compared with a series dredged at Acapulco, Mexico, in the H. N. Lowe Collection in the Museum of the San Diego Society of Natural History and with specimens

[26] *Tellina pumila* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 69. "Hab. Valparaiso; sandy mud, from seven to thirty fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 279, pl. 57, fig. 41. "Valparaiso."

*Tellina* (*Angulus*) *pumila* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 91, pl. 13, figs. 3 and 4. [Illustrations of holotype and paratype].

in the California Academy of Sciences. It appears from this study that Dall's type, 9 mm. in length, is a juvenile shell and that the species reaches a much larger size. A large right valve in the present collection dredged off El Salvador, measures: length, 18.3 mm.; height, 10 mm.; convexity (one valve), 2.6 mm.

The most striking features of this species are the ivory white color, iridescence in fresh shells and the flexuous posterior dorsal margin. This flexuosity is caused by the convexity of an area on the posterior dorsal margin just posterior to the ligamentary area. Some specimens are faintly tinted with pink on the umbonal area. Variation in the thickness and in the flexuosity of the posterior dorsal margin can be observed in a series of specimens. These features are most pronounced in the larger shells. The present specimens as well as a series in the Collections of the California Academy of Sciences from Panama Bay, a series in the same collection from Santa Elena Bay, Ecuador, collected by Woodbridge Williams, and a series in the H. N. Lowe collection from Acapulco, Mexico, show gradation from small, thin shells with a slightly flexuous posterior dorsal margin to fairly thick shells with strong flexuous posterior margins.

The hinge of this species is similar to that of *Tellina felix* except that the right anterior lateral is shorter and in the left valve the inner margin back of the beak is slightly thickened and some large specimens show traces of a left posterior lateral. The ivory color, longer posterior end and more convex posterior dorsal margin easily serve to separate this species from *T. felix*.

*Tellina hiberna* Hanley[27] appears to be a very similar shell. The illustrations of that species published by Hanley and Salisbury indicate that the shell is more abruptly sloping posteriorly, that there is a constricted area just anterior to the posterior umbonal ridge and anterior to this the shell is more expanded than in *T. tabogensis*.

*Distribution*: This species was dredged by the expedition off Meanguera Island, El Salvador, in the Gulf of Fonseca, where it occurred abundantly in 6 to 16 fathoms, off Corinto, Nicaragua, in 12-13 fathoms, and in the Gulf of Nicoya, Costa Rica, in 4-10 fathoms. It occurs north to the Gulf of California and south to Ecuador.

Subgenus ***Eurytellina*** Fischer.

KEY TO THE SPECIES OF *Eurytellina*.

A. Shell white or brownish
  a. Pallial sinus touching the anterior adductor impression
    b. Very elongate; adult valves with a median depressed area ventrally *planulata*
    bb. Shell high; without a median depressed area ventrally *laceridens*
  aa. Pallial sinus not touching anterior adductor impression
    c. Sculpture coarse, about 1 rib per millimeter *panamanensis*
    cc. Sculpture fine, about 3 ribs per millimeter *eburnea*

B. Shell entirely or partly some shade of pink or red
  a. Concentric sculpture of even strength over shell
    b. Pallial sinus confluent with a portion of the posterior margin of the anterior adductor impression *rubescens*
    bb. Pallial sinus not touching anterior adductor impression
      c. Concentric sculpture decussated by radial striae *princeps*[28]
      cc. Concentric sculpture not decussated, radial striae very fine or absent
        d. About 10 concentric grooves per millimeter *prora*
        dd. About 2 or 3 concentric grooves per millimeter
          e. Right valve with depressed area anterior to posterior umbonal angulation *simulans*
          ee. Right valve without depressed area anterior to posterior umbonal angulation
            f. Posterior dorsal area with strong concentric sculpture *mantaensis*
            ff. Posterior dorsal area with weak concentric sculpture or of growth lines only *ecuadoriana*[28]
  aa. Concentric sculpture of unequal strength over shell
    g. Posterior third of shell with coarse concentric lamellae giving way to fine striae anteriorly *inaequistriata*
    gg. Posterior third of shell smooth or nearly so in one or both valves, anteriorly sculptured with distant concentric grooves *regia*

***Tellina (Eurytellina) eburnea*** Hanley.

*Tellina eburnea* Hanley, *Proc. Zool. Soc. London*, September, 1844 p. 61, "Hab. Tumbez, Peru; in soft sandy mud, five fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 241, pl. 58, fig. 91. Tumbez, Peru. — Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 60, pl. 13, fig. 60. Original locality cited.

[27] See *Tellina hiberna* Hanley, Thes. Conch., Vol. 1, 1846, p. 282, pl. 57, fig. 53. "Panama; Bay of Guayaquil." —Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 13, figs. 7, 8, 9. [Illustrations of holotype and paratypes].

[28] Not represented in the present collection.

*Tellina* (*Peronaeoderma*) *eburnea* Hanley, Mörch, *Malakozool. Blätter*, Bd. 7, 1860, p. 186. Sonsonate, El Salvador.

*Type Locality*: Tumbez, Peru, in 5 fathoms, sandy mud.

*Range*: Gulf of California to Tumbez, Peru.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Nicaragua: Corinto, beach; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Oblong, solid, opaque, rather inequivalve, convex, whitish, glossy, clearly inequilateral, with strong deep concentric sulci, which usually become obsolete in one of the valves, and which diverge and become elevated on passing the flattened space at the upper edge of the more convex valve; ventral edge very slightly convex, curving obliquely upward anteriorly; posterior side much the shorter, subcuneiform; the ligamental edge straight, and abruptly sloping; ligament short and prominent; fold and umbonal ridge almost obsolete; inside pure white, teeth as in *punicea*. (Hanley, Thes. Conch., 1846).

The largest specimen in the present collection measures: length 28.3 mm.; height, 17.8 mm. The present specimens agree well with the younger stages of a specimen of *T. eburnea* in the collection at Stanford University which was collected in Ecuador by Stanley Herold, which measures: length, 47.5 mm.; height, 29.8 mm.; convexity (both valves together), 12.6 mm.

The concentric sculpture on the posterior dorsal areas becomes stronger and raised after crossing the umbonal ridge. This feature is emphasized by Hanley and Sowerby but it is not very pronounced on the present specimens.

*Tellina eburnea* is very similar to *T. alternata* Say, an east American species.

*Tellina laplata* Pilsbry & Olsson[29], described from the Pliocene of Peru, is also very similar to *T. eburnea*. Compared to *T. laplata* the present specimens do not show such strong raised sculpture on the posterior dorsal areas nor is the sculpture as strong on the left anterior dorsal area as that shown in the illustrations by Pilsbry & Olsson.

The shell of *Tellina eburnea* is higher in proportion to the length as compared to that of *T. simulans*, furthermore the color is pure white both exteriorly and interiorly. The general character of the pallial sinus is similar to that of *T. simulans*. It is somewhat higher behind and extends forward almost to but does not quite touch the anterior adductor impression and is confluent with the pallial line below. The hinge is similar to that of *T. simulans* except that the right posterior lateral is less distant from the cardinals. The sculpture is much finer and the pallial sinus extends nearer the anterior adductor impression than that of *T. panamanensis* Li.

*Distribution*: Specimens here referred to *Tellina eburnea* were dredged by the expedition in 13-40 fathoms, from off Guatemala and El Salvador, in the Gulf of Chiriqui, Panama, and were taken on the beach at Corinto, Nicaragua.

**Tellina (Eurytellina) inaequistriata** Donovan.

Plate I, Fig. 18.

*Tellina inaequistriata* Donovan, Nat. Hist. Brit. Shells, Vol. 4, 1802, pl. 123 [two figs.]. "A very rare species of *Tellina* communicated to Da Costa after his Conchology was published, and therefore not noticed in that work. It has been found by the late Dr. Pulteney we believe on the coast of Dorsetshire." – Chenu, Bibl. Conchyl., Ser. 1, Vol. 1, 1845, p. 82, pl. 32, figs. 7, 8. [French translation of Donovan's work on Shells]. – Hanley, Thes. Conch., Vol. 1, 1846, p. 238, pl. 57, fig. 58; pl. 58, fig. 80. "Bay of Guayaquil; (Cuming)."— Forbes & Hanley, Hist. Brit. Moll., Vol. 1, 1853 (issued August 1, 1848), p. 314. "Inhabits the Bay of Guayaquil; was introduced by Donovan, who only surmised that it had been taken by Dr. Pulteney on the Dorset coast."

*Tellina sanguinea* Wood, Gen. Conch., 1815, p. 159, pl. 44, fig. 2. "This shell is in the cabinet of Dr. Coombe." [No locality cited]. – Wood, Index Test., 1825, p. 18, pl. 4, fig. 27. Also ed. 1828. Locality unknown. Also ed. by Hanley, 1842-1856, p. 23, pl. 4, fig. 27. "Guayaquil." [States that fig. 80 in Thes. Conch. represents *T. sanguinea*]. – Hanley, Cat. Rec. Biv. Shells, 1843, p. 67.

*Tellina* (*Eurytellina*) *leucogonia* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 317, pl. 4, fig. 5. "Type. – No. 102182, U.S.N.M., from the Gulf of California, Stearns collection."

*Type Locality*: Bay of Guayaquil, Ecuador (according to Hanley and Forbes & Hanley). [Erroneously cited from the coast of Dorsetshire, England, by Donovan].

*Range*: Gulf of California to the Bay of Guayaquil, Ecuador. Caribbean (Dautzenberg).

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-19-21), 17-18 fathoms, mud, gr. mud, crushed shell; Tangola-Tangola Bay (196-D-13), 10 fathoms, gr. sand, crushed shell; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud.

*Description*: Shell ovate, compressed and rather flattish, rosy, very finely striated transversely: the striae fewer and larger at the anterior [posterior] end (Donovan).

Shell elongate, moderately thick, somewhat compressed, glossy, subequilateral, red or orange-red; a well-defined fairly broad posterior area is set off by a rounded post-umbonal ridge; posterior dorsal margin slightly rounded, sloping downward and slightly expanded along the ventral half; the ornamentation consists of concentric striae which, especially on the right valve, are very

[29] *Tellina* (*Eurytellina*) *laplata* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 67, pl. 15, figs. 1-5. "Canoa formation, Punta Blanca." Ecuador. Pliocene.

strongly developed and widely spaced on about the posterior third of the shell then change abruptly to fine striae anteriorly; hinge normal for the subgenus; the pallial sinus does not quite touch the anterior adductor impression but is separated by a narrow area, wholly confluent with the pallial line below and, in general features, similar to that of *T. simulans* and *T. prora*.

A right valve in the present collection from Santa Cruz Bay, Mexico, measures: length, 23 mm.; height, 12.5 mm. It agrees well with Hanley's plate 50, figure 80. Other specimens in the collection are similar but show the strong sculpture only slightly developed anterior to the angulation.

Some of the small shells, especially left valves, almost lack strong concentric sculpture anterior to the posterior area; in such cases they may be ornamented only by faint grooves slightly out of harmony with the incremental lines.

A series of specimens in the H. N. Lowe collection of the San Diego Society of Natural History, varying in length from approximately 8.5 mm. to 26.2 mm. and identified by Lowe as *Tellina leucogonia* Dall, are identical with the present specimens. The present series together with Lowe's specimens show all variations from young smooth shells up to a large right valve with the typical sculpture of *T. inaequistriata*. We are therefore inclined to consider Dall's species as identical with *T. inaequistriata*.

The very distinct concentric sculpture, changing from coarse to fine at about the posterior third of the shell, serves to separate this form from similar west American species of the genus.

*Tellina waylandvaughani* Maury[30], described from the Miocene of Santo Domingo, is a similar species.

*Distribution*: Specimens of this species were dredged by the expedition in 10 to 18 fathoms from off western Mexico and Costa Rica. The present records of occurrence show the range of this species to extend from the Bay of Guayaquil north to the Gulf of California. Dautzenberg[31] cited *Tellina inaequistriata* as occurring in the Caribbean region at the Island of Martinique and in Venezuela. He stated that he could detect no differences which would serve as a basis for separating the Caribbean shells from those illustrated under that name from the Bay of Guayaquil.

**Tellina (Eurytellina) laceridens** Hanley.

*Tellina laceridens* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab. Tumbez, Peru; soft sandy mud, five fathoms." "Var. testa, magis trigona . . ." "Hab. chiriqui, West Columbia; sandy mud, three fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 243, pl. 61, figs. 168, 176. [Not. pl. 66, fig. 258.]. Original localities cited. —Sowerby, Conch. Incon., Vol. 17, *Tellina*, 1867, species 104, pl. 20, fig. 104. Tumbez, Peru.

*Type Locality*: Tumbez, Peru, in 5 fathoms, soft, sandy mud.

*Range*: Realejo [near Corinto], Nicaragua, to Tumbez, Peru.

*Collecting Stations*: Nicaragua: Corinto, beach; Costa Rica: Port Culebra; Colombia: Gorgona Island.

*Description*: Shell elongately trigonal, beaks nearly central but slightly anteriorly placed, posterior end obliquely truncated; sculpture of fine, concentric grooves which in places are irregular, the umbonal region, and often the posterior area, relatively smooth; white, sometimes with a pinkish spot on the umbonal region; ligament large, exterior; hinge with cardinals grooved, especially the right posterior cardinal which appears ragged due to 7 to 10 grooves; the pallial sinus touches the anterior adductor impression just above the base; interior white and yellow and in large specimens with somewhat granular areas and salmon pink spots.

A specimen collected at Gorgona Island, Colombia, measures: length, 53 mm.; height, 34.8 mm.; convexity (both valves together), 11.6 mm.

Some of the characters in which this species differs from *Tellina panamanensis* Li are: the finer concentric sculpture, larger smooth umbonal area, regular sculpture along the posterior dorsal margin and in that the pallial sinus touches the anterior adductor impression.

*Distribution*: A few specimens of this species were collected by the expedition in the beach drift at Corinto, Nicaragua, one at Port Culebra, Costa Rica, and one at Gorgona Island, Colombia. It also has been recorded as occurring in beds of Pliocene age in Panama.

**Tellina (Eurytellina) mantaensis** Pilsbry & Olsson.

*Tellina (Eurytellina) mantaensis* Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 80, pl. 8, figs. 1-4. "Manta, Ecuador."

*Type Locality*: Manta, Ecuador.

*Range*: Gulf of Chiriqui, Panama, to Manta, Ecuador.

*Collecting Station*: Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell elongated, rather compressed, the anterior end slightly the longer, posterior end obliquely subtruncated; sculpture of flat concentric ridges which are separated by narrower grooves; the posterior area is usually ornamented by waved raised threads and with faint radial lines on one or the other valve; hinge of right valve with a strong anterior lateral adjacent to the cardinals and a more distant posterior lateral, the laterals are smaller in the left valve; the pallial sinus reaches almost to the anterior adductor impression and in this character is similar to *T. simulans*,

[30] *Tellina waylandvaughani* Maury, *Bull. Amer. Paleo.*, Vol. 5, No. 29, 1917, p. 386 (222), pl. 64 (38), figs. 7 and 8. "Zone G. Rio Gurabo at Los Quemados." Santo Domingo. Miocene.

[31] Dautzenberg, P., *Mem. Zool. Soc. France*, Vol. 13, 1900, p. 260.

and is confluent with the pallial line below; fresh specimens are rose colored, more deeply on the umbos, and somewhat brownish colored ventrally.

Two valves in the present collection agree well with the illustrations of *T. mantaensis* Pilsbry & Olsson. The larger specimen measures approximately 21 mm. in length and 15 mm. in height.

The shell of this species differs from that of *Tellina simulans* in that it is more elongated and the dorsal margins slope more gently, especially posteriorly where the area is somewhat flattened. There also are differences in the details of the hinges of the two species. The right posterior cardinal of *T. mantaensis* reaches almost to the ventral margin of the hinge plate which beneath that tooth is strongly indented. In *T. simulans* the corresponding tooth reaches little more than halfway to the ventral margin of the hinge plate which at that point is gently rounded.

The strong concentric sculpture on the posterior dorsal area and more gently sloping anterior dorsal margin are features which serve to separate this species from *T. ecuadoriana* Pilsbry & Olsson.

*Distribution*: Two single valves of this species were taken by the expedition in 30-40 fathoms on a bottom of sandy mud in the Gulf of Chiriqui, Panama. This is an extension north of the known range of the species.

**Tellina (Eurytellina) panamanensis** Li.

*Tellina panamanensis* Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 262, pl. 5, fig. 32. " 'Brought up by marine dredge from depths varying from 10. ft. to 40. ft. in the mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay.' " "Horizon: Gatun formation." —Pilsbry, *Nautilus*, Vol. 58, No. 4, April, 1945, p. 145.

*Tellina* (*Eurytellina*) *panamanensis* Li, Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, November 13, 1931, p. 436, pl. 41, figs. 4, 5, 6. A Recent shell from Panama Bay.

*Tellina liana* Hertlein & Strong, *Nautilus*, Vol. 58, No. 3, January, 1945, p. 105. "Dredged off Meanguera Island, El Salvador, in the Gulf of Fonseca, in 16 fathoms."

*Type Locality*: Mouth of Rio Grande near La Boca about 1 mile from the mainland in Panama Bay, 10-40 feet, mud.

*Range*: Tenacatita Bay, Mexico, to the Bay of Panama.

*Collecting Stations*: Mexico: Tenacatita Bay (183-D-2), 30 fathoms, muddy sand; Port Guatulco (195-D-20, 21), 18-23 fathoms, mud; Tangola-Tangola Bay (196-D-17, 18), 23-30 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell similar in general outline to that of *Tellina laceridens* but more steeply truncated posteriorly; the left valve is more convex and overlaps the right along the right anterior dorsal margin; a faint broad median concavity is present toward the ventral margin of the valves; color grayish-white covered by a thin ochraceous periostracum; the concentric sculpture consists of ridges (about 1 per millimeter) which on their upper portions are flat, on the lower sloping, crossed by fine weak radial striae; on the right valve a ridge or angulation occurs from beak to base posteriorly; on the posterior dorsal area the concentric sculpture is usually sinuated, sometimes bent back, due to the presence (although sometimes absent) of a median radial convexity; hinge with two cardinals and two laterals in each valve, the right anterior cardinal grooved, the posterior with about four sulcations, the anterior lateral close to the cardinals, the posterior lateral distant about one-third the length of the posterior dorsal margin; left valve with the anterior cardinal grooved, the posterior cardinal a thin lamella, laterals weak; pallial sinus highest beneath the beaks, descending to a broadly rounded or blunt point which is well separated from and lower than but posterior to the anterior adductor impression, along the base confluent with the pallial line. Dimensions of a typical specimen: length, 44.9; height, 29 mm.; convexity (both valves together), 13 mm.; pallial sinus extends anteriorly 34.5 mm. from posterior end of shell.

The shell of this species differs from that of *Tellina laceridens* in the more steeply sloping posterior dorsal margin, more convex valves, much coarser sculpture which, especially on the left valve, is sinuated on the posterior dorsal area, in the smaller smooth area at the beaks, less crenated cardinal teeth and in that the pallial sinus does not touch the anterior adductor impression but is separated from it by a considerable distance. The much coarser sculpture and the much greater distance between the pallial sinus and the anterior adductor impression are features separating it from *T. eburnea*.

*Distribution*: Specimens of *Tellina panamanensis* were dredged by the expedition from Tenacatita Bay, Mexico, to Meanguera Island, El Salvador, in 16-30 fathoms. This record of Tenacatita Bay, Mexico, is an extension north of the known range of the species. It also has been recorded as occurring in the Pliocene of Ecuador.

**Tellina (Eurytellina) planulata** Sowerby.

Plate I, Fig. 22.

*Tellina planulata* Sowerby, Conch. Icon., Vol. 17, *Tellina*, June, 1867, species 186, pl. 33, fig. 186. "Hab. —?"

*Type Locality*: Gulf of Dulce, Costa Rica (here designated as type locality). No locality originally cited.

*Range*: La Libertad, El Salvador, to the Gulf of Dulce, Costa Rica.

*Collecting Stations*: El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Costa

Rica: Gulf of Dulce; Golfito Bay, Gulf of Dulce.

*Description*: Shell elongate, the posterior end the longer, fairly thick, white, similar to *Tellina laceridens* in general features but longer in proportion to the height; sometimes with a low broad medial depression toward the ventral margin; posterior dorsal area set off by a slight angulation; sculpture consisting of very fine, shallow, somewhat irregularly spaced concentric grooves; right valve with two grooved cardinals, anterior lateral close to the cardinals but the posterior lateral distant about half the length of the posterior dorsal margin; left valve with a grooved anterior cardinal and posterior to this two small, thin, laminae, laterals small; the pallial sinus projects anteriorly and barely touches the base of the anterior adductor impression, along the base it is confluent with the pallial line.

A left valve measures: length, 59.2 mm.; height, 33 mm.; convexity (one valve), 6 mm.

Several single valves from the Gulf of Dulce agree so closely with Sowerby's description and figure of *Tellina planulata* that we have assigned our specimens to that species. This species was originally described without information as to the locality from which it came. Paetel[32] cited the species as occurring at "Sitka," Alaska, but we have not seen any specimens from that region which appear to be referable to it. Other than Paetel's record the species apparently has not been recognized as occurring elsewhere. We therefore have designated the Gulf of Dulce as type locality. Sowerby stated that it is "A much larger and flatter shell than *Tellina eburnea*, with closer grooves and no transverse ridges on the dorsal margin of the overlapping valve." Those differences are true with regard to the present specimens. The pallial sinus in the present specimens touches the anterior adductor impression whereas in *T. eburnea* it is separated from the corresponding impression by a narrow space. Sowerby stated with regard to the posterior end: "terminal margin notched." This latter feature is not pronounced on our specimens but they are not perfectly preserved.

The present specimens closely resemble *Tellina ecuadoriana* Pilsbry & Olsson[32a] described from Ecuador. A single valve of that species collected by the senior author at Corinto, Nicaragua, is in the collections of the California Academy of Sciences.

Compared to *Tellina ecuadoriana* the posterior dorsal margin of *T. planulata* slopes a little more steeply and the posterior area, especially on the right valve, appears to be a little narrower than the corresponding area on the species described by Pilsbry & Olsson. The shell of the present species is white rather than rose red with whitish zones. Furthermore the pallial sinus in the present specimens touches the anterior adductor impression while in *T. ecuadoriana* the two are separated by a narrow space.

*Distribution*: Several valves of this species were collected by the expedition on the beach in the Gulf of Dulce, Costa Rica. One small specimen with both valves was dredged in 14 fathoms off La Libertad, El Salvador.

### *Tellina (Eurytellina) prora* Hanley.

*Tellina prora* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab Porto St. Elena, West Columbia; sandy mud, six fathoms; and Salango, West Columbia, sandy mud, nine fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 243, pl. 60, fig. 152. Original localities cited. — Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1866, species 90, pl. 18, fig. 90. Original localities cited. —Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 86. "The shell ranges through the south of the Panamic and north of the Peruvian areas."

*Tellina cibaoica* Maury, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, 1930, p. 261, pl. 4, fig. 30. Dredged in Panama Bay. Referred to the Gatun formation, Miocene. According to Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430), Li's record was based upon "A left valve of *Tellina prora* Hanley"...

Not *Tellina cibaoica* Maury, 1917. Santo Domingo, Miocene.

*Type Locality*: Santa Elena, Ecuador, in 6 fathoms, sandy mud (here designated as type locality). Salango, Ecuador, in 9 fathoms, sandy mud, also originally cited by Hanley.

*Range*: Mazatlan, Mexico, to the Bay of Guayaquil, Ecuador.

*Collecting Stations*: Mexico: Tangola-Tangola Bay (196-D-17), 23 fathoms, mud; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union, Gulf of Fonseca (199-D-15), 6 fathoms, mud; Nicaragua: Potosi and Monypenny Point; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; Panama: Bahia Honda (222-D-5), 11 fathoms, mud, shells, leaves.

*Description*: Shell ovately trigonal, smooth, polished, a posterior area set off by an angulation, colored rose pink with whitish concentric bands; sculpture of very fine closely spaced (about 10 per millimeter) incised concentric striae; hinge with two grooved cardinals in each valve, the left posterior one very narrow, two laterals in each valve, those in the left valve much the smaller; pallial sinus highest in middle part of shell, usually separated from the anterior adductor impression by about a millimeter

[32] Paetel, Fr., Cat. Conchyl.—Samml., Vierte Neubearbeitung (Berlin: Verlag von Gebrüder Paetel), Abt. 3, 1890, p. 49.

[32a] *Tellina (Eurytellina) ecuadoriana* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 67, pl. 15, figs. 6, 7, 8. Canoa formation, Punta Blanca. Ecuador, Pliocene. Also Recent, Santa Elena, Ecuador (type), also at Canoa and Callo, the port of Jipijapa.

but sometimes almost, but not quite, touching, the end blunt and almost in line vertically below the posterior side of the adductor impression, along the base confluent with the pallial line.

A large specimen dredged off Guatemala measures approximately: length, 46.4 mm.; height, 17.5 mm.; convexity (both valves together), 12 mm.

The shell of this species differs from that of *Tellina rubescens* Hanley in that the posterior slope is more gently inclined, the concentric incised striae are much finer and much more closely spaced and the pallial sinus does not touch the anterior adductor impression. The very much finer and more closely spaced concentric sculpture easily serves to separate the species from *T. simulans* C. B. Adams.

The record of *Tellina prora* from the Cape Verde Islands in the Atlantic cited by Rochebrune[33] can be referred to some other species. *Tellina (Eurytellina) trinitatis* Tomlin[34], described from Colon Harbor on the east side of the isthmus of Panama, is said to be similar to *T. prora*.

*Distribution*: This species was collected by the expedition off western Guatemala, El Salvador and Nicaragua, in 6-14 fathoms on a muddy bottom. It also has been recorded as occurring in the Pliocene of Ecuador.

### *Tellina (Eurytellina) regia* Hanley.

*Tellina regia* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 61. "Hab. Real Llejos, Central America; in coarse sandy mud, seven fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 240, pl. 60, fig. 140. Original locality cited.

*Type locality*: Real Llejos [near Corinto], Nicaragua, in 7 fathoms, coarse, sandy mud.

*Range*: Known only from the type locality and vicinity.

*Collecting Station*: Nicaragua: Corinto, beach drift.

*Description*: Oblong, thin, rather compressed, almost inequivalve, subequilateral; extremely glossy, both externally and internally of a deep subpellucid purplish crimson; the surface marked with distant concentric grooves, which posteriorly become obsolete in one or both of the valves; the ventral edge nearly straight, subretuse in the middle; anterior side slightly shorter, its extremity obtusely rounded; posterior extremity almost biangulated; dorsal moderately and almost equally sloping on either side of the beaks, nearly straight posteriorly; umbonal ridge and flexure nearly obsolete; the ligament rather prominent; teeth as in *punicea*. (Hanley, Thes. Conch., 1846).

A left valve from Corinto, Nicaragua measures approximately: length, 17 mm. height, 10 mm.; convexity (one valve), 1.8 mm.

The outline as well as the other features of the present specimen are similar to those described for *Tellina regia* which came from the same general vicinity. The concentric ornamentation of the shell is like that decribed for *T. regia*, namely, distant concentric grooves which become obsolete posteriorly.

*Tellina regia* differs from *Tellina rubescens* in that the concentric grooves become obsolete posteriorly, the dorsal margins do not slope so steeply, and the pallial sinus does not touch the anterior adductor impression. It differs from *Tellina princeps* in lacking radial striae.

*Distribution*: Only one valve referred to this species was found in the beach drift at Corinto, Nicaragua.

### *Tellina (Eurytellina) rubescens* Hanley.

*Tellina rubescens* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 60. "Hab. Panama and Tumbez; in sandy mud."—Hanley, Thes. Conch., Vol. 1, 1846, p. 242, pl. 60, fig. 153. Tumbez, and Panama (Cuming). —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1866, species 93, pl. 18, fig. 93. "Hab. Tumbez and Panama, Peru."

*Type Locality*: Panama in sandy mud (here designated as type locality). Tumbez, Peru, in sandy mud, also originally cited.

*Range*: Tenacatita Bay, Mexico, to Tumbez, Peru.

*Collecting Stations*: Mexico: Tenacatita Bay; El Salvador: La Union, Gulf of Fonseca (199-D-12), 5 fathoms, mud; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Costa Rica: Port Parker.

*Description*: Shell trigonally ovate, smooth, polished, colored exteriorly and interiorly by light and darker concentric bands of rose pink; posterior dorsal margin sloping steeply, the area set off by an angulation; sculpture consists of fine concentric grooves (about 2 per millimeter) and between these finer concentric striae, the whole crossed by very fine submicroscopic radial striae; hinge with two cardinals and two laterals in each valve, the right anterior cardinal usually grooved, the posterior bifid, left anterior grooved, the posterior one thin, laterals in left valve weak; anterior end of pallial sinus confluent with the lower posterior margin of the anterior adductor impression from a point just above the base to approximately the middle of the base of the impression, confluent with the pallial line below.

A large specimen from the Gulf of Fonseca measures: length, 43 mm.; height, 37 mm.; convexity (both valves together), 9.3 mm.

The shell of *Tellina rubescens* differs from that of *T. prora* Hanley in that it is higher

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33 *Peronaeoderma prora* Hanley, Rochebrune. *Nouv. Arch. Mus. d'Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 258. "Hab.—Rade de Saint-Vincent." Cape Verde Islands.

34 *Eurytellina trinitatis* Tomlin, *Jour. Conch.*, Vol. 18, No. 11, July, 1929, p. 310. "Hab. Colon Harbour, not uncommon, dead but very fresh in 5 f."

in proportion to the length, the posterior dorsal margin slopes more steeply, the incised concentric sculpture is more widely spaced and the pallial sinus is confluent with a portion of the posterior side of the anterior adductor impression. These same characters of proportionate height to length and that of the pallial sinus serve to separate *T. rubescens* from *T. simulans* C. B. Adams, a species in which the concentric sculpture is much more strongly developed.

*Distribution*: This species was taken by the expedition along the west coast of Mexico and Central America but at no place abundantly. It also has been recorded by Arnold, 1903, as occurring in the upper Pleistocene of San Pedro, California. Some of the records of the occurrence of this species at San Ignacio Lagoon and at Magdalena Bay, Lower California, are referable to *T. simulans*.

**Tellina (Eurytellina) simulans** C. B. Adams.

*Tellina simulans* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 508, 546 (separate pp. 284, 322). "Panama." Also cited from Xipixapi, Ecuador, in sandy mud at 10 fathoms. —Römer, Neues Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 4, *Tellina*, 1872, p. 99, pl. 25, figs. 4, 5.

*Tellina punicea* Born, Carpenter, Cat. Mazatlan Shells, August, 1855, p. 35. Mazatlan, Mexico. Also earlier records cited. —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1866, species 53, pl. 12, fig. 53. "Hab. Xipixapi, W. Columbia; in sandy mud, ten fathoms; H. Cuming."

Not *Tellina punicea* Born, Test. Mus. Caes. Vind., 1780, p. 33, pl. 2, fig. 8. "Patria ignota." [Now believed to be a Caribbean species. See Gardner, *U. S. Geol. Surv., Prof. Paper* 142-*E*, 1928, p. 193].

*Tellina costaricana* Olsson, Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930 p. 262, pl. 4, fig. 31. Dredged in Panama Bay at mouth of Rio Grande River in 10-40 ft. "Occurrence: Gatun Stage, Banana River, Costa Rica." "Horizon: Gatun formation." This record is based upon "Two valves of *Tellina simulans* C. B. Ad.," Panama, Recent, according to Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 430).

*Type Locality*: Panama.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to Tumbez, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California; Tenacatita Bay; 17 miles SE. × E. of Acapulco (189-D-3), 13 fathoms, mud; Nicaragua: Corinto (200-D-11, 19), 8-13 fathoms, sand, mangrove leaves; Costa Rica: Culebra Bay; 1 mile south of Golfito.

*Description*: Shell elongately oval, posterior dorsal margin obliquely sloping, the end obliquely truncated and slightly bent to the right, rose pink with whitish concentric bands; posterior area set off by an angulation anterior to which is a shallow broad depressed area on the right valve, the posterior area bears a narrow, shallow, radial furrow which is especially noticeable on the left valve; sculpture of regular, deep, concentric grooves (about 2 or 3 per millimeter) and very fine submicroscopic radial striae; hinge with anterior laterals close to the cardinals, posterior laterals distant, weaker in left valve; the pallial sinus does not quite touch the anterior adductor impression, the end is blunt and almost in line vertically below the posterior margin of the adductor impression, along the base it is confluent with the pallial line.

A large specimen of this species in the Henry Hemphill Collection of the California Academy of Sciences from Magdalena Bay, Lower California, measures: length, 48.8 mm.; height, 29 mm.; convexity (both valves together), 11 mm.

This species, in some instances, has been cited in the earlier literature under the names of *Tellina punicea* Born and *T. rubescens* Hanley.

The shell of this species differs from that of *T. rubescens* in the greater length in proportion to the height, in the much deeper, stronger and more widely spaced concentric sculpture and in that the pallial sinus does not touch the anterior adductor impression.

*Tellina simulans* is similar to *T. angulosa* Gmelin (*T. punicea* of some authors), an east American species; in fact Carpenter and others considered the two to be identical. According to Adams *T. simulans* differs from the east American species in that "its furrows are deeper and are continued over the flexure, without change of depth; the interspaces are less flattened, and the lateral teeth are nearly obsolete." A comparison of specimens of *T. simulans* with a series of *T. angulosa* collected by F. M. Anderson at Cartagena Bay, Colombia, shows differences between the two. The west coast shells are more pointed posteriorly, there is a low depressed area anterior to the posterior angulation on the right valve, and the concentric grooves along the posterior dorsal margin bend more acutely upward than on the east coast shells.

*Tellina princeps* Hanley, described from Tumbez, Peru, is a distinct species possessing a large, red, subequilateral shell with a gently sloping posterior dorsal margin and the concentric sculpture is crossed by strong radial striae.

*Distribution*: This species was taken by the expeditions although not abundantly, from Santa Inez Bay, in the Gulf of California to Culebra Bay, Costa Rica. It ranges south to Peru. It also is known to occur in the Pleistocene at San Ignacio Lagoon and at Magdalena Bay, Lower California.

Subgenus **Tellinidella** Hertlein & Strong, subgen. nov.

Type: *Tellinides purpureus* Broderip & Sowerby.

Shell elongate, compressed, very thin,

with a strong posterior angulation; ornamented with fine concentric granulated ridges which are crossed by impressed radial striae forming reticulate sculpture; hinge as in *Eurytellina* but with a very small right anterior lateral and a weak posterior lateral, in the left valve the laterals are faint or obsolete.

The general outline and hinge of this new subgenus are similar to those of *Eurytellina*. The weak distant right posterior lateral and the very thin shell, which is ornamented by both concentric and radial sculpture, are characteristic features of the type species of *Tellinidella*.

Dall, 1900, placed *Tellina purpureus* Broderip & Sowerby in the subgenus *Tellinides* Lamarck[35]. That name was proposed by Lamarck for a genus of *Tellina* with the sole species *T. timorensis* as type. No illustrations accompanied that work. Dubois[36] discussed Lamarck's genera but he did not illustrate the type species of *Tellinides*. Neither did Delessert, 1841, include *T. timorensis* among his illustrations of the types of Lamarck's shells. Hanley[37] later gave illustrations showing two views of the exterior of right valves of *T. timorensis*. Philippi[38] also illustrated a species under that name and gave views of both the exterior and interior of the right valve and an umbonal view of both valves. His illustrations agree well with Lamarck's description of the species. Bertin[39], 1878, stated that 4 type specimens of Lamarck's species were present in the collections of the Museum of Natural History in Paris. In his synonymy of the species he included references to Hanley's figures 158 and 172, Philippi's figure 3, as well as illustrations of Römer's, 1812, plate 34, figures 4-6.

It appears then that these figures may be considered to represent authentic specimens of *T. timorensis*. The right valve has two diverging cardinal teeth, a close anterior lateral and a weak close posterior lateral. The left valve is said to lack laterals. The valves are not flexed posteriorly and the posterior umbonal fold or ridge is broadly rounded and nearly obsolete.

The hinge of the right valve of *Tellina purpureus* has two diverging cardinal teeth, the posterior one strong and bifid or grooved. The posterior lateral is distant from the cardinals. A small lamina sometimes occurs near the margin above the small anterior lateral and sometimes the margin is somewhat projecting just over the posterior lateral. Furthermore the shell has a strong, angular posterior umbonal fold exteriorly and the concentric sculpture on the shell is decussated by radial grooves giving it a finely granulose character. These characters on the present shell are so different from those of *T. timorensis* that we propose a new subgenus *Tellinidella* with *Tellina purpureus* Broderip & Sowerby as type.

**Tellina (Tellinidella) purpureus** Broderip & Sowerby.

*Tellinides purpureus* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 363. "Hab. ad littora Oceani Pacifici." — Sowerby, Zool. Beechey's Voy., 1839, p. 153, pl. 42, fig. 2. "Inhabits the sandy shores of the Pacific Ocean."

*Tellina* (*Tellinides*) *purpurascens* Broderip & Sowerby, Hanley, Thes. Conch., Vol. 1, 1846, p. 295, pl. 62, fig. 194. "Real Leijos [Llejos] Central America (Cuming)."

Not *Tellina purpurascens* Gmelin, Linn. Syst. Nat., ed 13, Vol. 1, Pt. 6, 1790, p. 3237. Habitat not cited. Ref. to Lister, Conch., pl. 391, fig. 230. Also "B" and "Y," ref. to Gualtieri, Test., pl. 77, figs. L? and M? *Tellina purpurata* is described on p. 3243. Hab. not cited. Ref. to Gualtieri, Test., pl. 77, fig. L.

*Tellina broderipii* "Desh. ms. (teste Cum.)" Carpenter, Cat. Mazatlan Shells, August, 1855, p. 32. "Mazatlan."

*Tellina purpurascens* Broderip & Sowerby, Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 103, pl. 20, fig. 103. Same locality as given by Hanley.

*Type Locality*: Real Llejos [near Corinto], Nicaragua (here designated as type locality). Shores of Pacific Ocean originally cited.

*Range*: Altata, Mexico, in the Gulf of California, to Colombia.

*Collecting Stations*: Mexico: Tenacatita Bay; Sihuatanejo Bay; Nicaragua: Corinto, beach drift.

*Description*: Shell ovately oblong, subequilateral, thin, compressed, colored a beautiful purplish-rose with the dorsal margins white; sculpture of close, decussating concentric and radial striae; posteriorly a low radial furrow is present near the dorsal margin which anteriorly is bounded by a low carina; right valve with two cardinals, the posterior one the larger and bifid, and a very close, small, anterior lateral above which there is sometimes a small lamina near the margin, and a posterior lateral distant nearly half the length of the posterior dorsal margin, above this tooth the margin is sometimes somewhat projecting; left valve with laterals obsolete; the end of the pallial sinus is considerably lower than and posterior to the anterior adductor impression, the base is confluent with the pallial line.

A right valve from Tenacatita Bay, Mexico, measures: length, 49.4 mm.; height, 26.4 mm.; convexity (one valve), 4 mm.; pallial

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35 *Tellinides* Lamarck, *Hist. Nat. Anim. s. Vert.*, Vol. 5, July, 1818, p. 535. Type, *Tellina timorensis*, p. 536. "Habite l'océan des grandes Indes ou austral, prés de Timor."

36 Dubois, C., Epit. Lamarck's Arrang. Test., 1824, p. 58.

37 *Tellina* (*Tellinides*) *timorensis* Lamarck, Hanley, Thes. Conch., Vol. 1, 1846, p. 292, pl. 61, figs. 158 and 172. Isle of Negros, Philippines, etc.

38 *Tellina timorensis* (*Tellinides*) Lamarck, Philippi, *Abbild. u. Beschreib. Conchyl.*, Bd. 2, Heft 4, *Tellina*, August, 1846, p. 90 (22), pl. 4, fig. 3. Timor, Philippine Islands, Sumatra, etc.

39 Bertin, V., *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 1, 1878. p. 283. [He mentioned that *T. timorensis* is represented in the collection by specimens including "par 4 individus ordinaires de Timor (types de Lamarck)."]

sinus extends forward 36 mm. from the posterior end of the valve. The species attains a greater size than this specimen.

The original name for this species, given by Broderip & Sowerby in 1829, was *Tellinides purpureus*. Dall[40] apparently considered that combination of names preoccupied due to the fact that *Tellinides* is now considered to be a subgenus of *Tellina*, also the fact that Dillwyn[41] had referred to a *Tellina purpurea*.

However, Dillwyn in a footnote, in remarking on certain of Gmelin's species, referred to Gmelin, page 3243, and on that page of Gmelin's work the species was cited as *Tellina purpurata*. It thus appears that Dillwyn's spelling of "*purpurea*" was a misprint and not a renaming of Gmelin's species. If this view is accepted, there then appears to be no valid reason for rejecting the original name given the west American species by Broderip & Sowerby. The name *Tellina purpurascens* which Hanley used for this species is preoccupied by *Tellina purpurascens* Gmelin, 1790. The name *Tellina broderipii* attributed to Deshayes was applied to the west American form by Carpenter.

The shell of this species bears a resemblance to that of *Tellina princeps* Hanley[42] but is thinner, narrower, the posterior dorsal margin slopes more gently, the radial striae are stronger and the right posterior lateral is weaker.

*Distribution*: A few specimens of this species, nearly all right valves, were taken by the expedition along the coast of west Mexico and in the beach drift at Corinto, Nicaragua.

Subgenus **Macaliopsis** Cossmann.

KEY TO THE SPECIES OF *Macaliopsis*.

A. Beaks directed strongly anteriorly; concentric lamellae about 1 per mm. ..... *lyra*

B. Beaks directed only slightly anteriorly; concentric lamellae, lower, fewer, usually about 3 per mm. ..... *lyrica*

**Tellina (Macaliopsis) lyra** Hanley.

*Tellina lyra* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 68. "Hab. Tumbez, Peru."—Hanley, Thes. Conch., Vol. 1, 1846, p. 271, pl. 62, fig. 187. Tumbez, Peru. —Sowerby, Conch. Icon., Vol. 17, *Tellina*, September, 1867, species 203, pl. 36, fig. 203. Tumbez, Peru.

*Type Locality*: Tumbez, Peru.

*Range*: Lower California to Tumbez, Peru (Dall).

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-2), 14 fathoms, mud,

*Description*: Shell elliptic, thin, compressed, slightly longer anteriorly, dull white exteriorly and interiorly, beaks curved forward; anterior dorsal margin excavated below the beaks, anterior end rounded, ventral margin broadly rounded, the posterior dorsal margin nearly straight or very broadly curved and sloping posteriorly directly from the beaks; a deep smooth lunule and escutcheon present; the sculpture consists of regular, thin, sharp, raised, concentric ribs which are separated by much wider interspaces (about 1 mm. wide) but which become narrower toward the ventral margin, a narrow posterior area is set off by an umbonal carina; hinge of right valve with a strong grooved triangular posterior and a thin anterior cardinal near the margin, a strong anterior and posterior lateral present; left valve with a grooved anterior and a thin posterior cardinal tooth and lateral triangular projections of the nymph; the pallial sinus extends for about three-fifths the length of the shell, subtrigonal above and highest just posterior to a line vertical with the beaks, then descending and narrowly elliptically rounded anteriorly then bending posteriorly and for about two-thirds of its length confluent with the pallial line.

The largest specimen in the present collection, a left valve, measures: length, 50 mm. height, 35 mm.; convexity (one valve), 6 mm.; pallial sinus extends anteriorly 29 mm. from the posterior end of the valve.

The strongly anteriorly directed beaks, more convex anterior dorsal margin which is excavated beneath the beaks, higher and more widely spaced concentric sculpture and shorter and more trigonal pallial sinus are features separating this species from *Tellina lyrica* Pilsbry & Lowe.

*Tellina protolyra* Anderson[43] is a similar species but it is smaller, less elongate, more inflated and the posterior dorsal margin is straighter than in the present species.

*Tellina (Macaliopsis) aequizonata* Pilsbry & Olsson[44], described from the Pliocene of Ecuador, is said to be much larger, more strongly sculptured and more circular in outline than *T. lyra*.

*Distribution*: A few specimens, mostly single valves, of this interesting species were dredged in 14 fathoms off Guatemala and El Salvador on a mud bottom.

**Tellina (Macaliopsis) lyrica** Pilsbry & Lowe.

*Tellina (Macaliopsis) lyrica* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*,

[40] Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302.

[41] Dillwyn, L. W., Descript. Cat. Rec. Shells, Vol. 1, 1817, p. 72, footnote.

[42] *Tellina princeps* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 62. "Hab. Tumbez, Peru; soft sandy mud, five fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 238, pl. 63, fig. 206. "Tumbez, Peru; (Cuming)." —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 135, pl. 25, fig. 135. Tumbez, Peru. —Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, 1934, p. 91, pl. 9, fig. 4. [Illustration of type].

[43] *Tellina protolyra* F. M. Anderson, *Proc. Calif. Acad. Sci.*, Ser. 4, Vol. 18, No. 4, March 29, 1929, p. 174, pl. 21, figs. 2, 3. "From Loc. 267-B, C. A. S., horizon M-N, of the Tuberá group, Colombia; Miocene."

[44] *Tellina (Macaliopsis) aequizonata* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 68, pl. 14, fig. 7. "Jama formation, Puerto Jama." Ecuador. Pliocene.

Vol. 84, May 21, 1932, p. 94, pl. 10, figs. 4, 4a. "Guaymas in about 20 fathoms."

*Type Locality*: Guaymas, Mexico, in about 20 fathoms.

*Range*: Gulf of California to the Gulf of Chiriqui, Panama.

*Collecting Stations*: Mexico: Santa Inez Bay in the Gulf of California (143-D-3, 4), 25-35 fathoms, mud, crushed shell, sand; El Salvador: La Libertad (198-D-2), 14 fathoms, mud; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell transversely oval, beaks turned slightly forward, anterior end broadly rounded, posterior dorsal margin broadly curved and rather steeply sloping; a slight angulation sets off a narrow posterior area; lunule smooth, slightly sunken; escutcheon deeply sunken and bounded by a high keel; sculpture consists of fine, close, concentric ribs (about 3 per millimeter) which are narrower than the interspaces; right valve with a simple anterior and grooved posterior cardinal and well-developed laterals, the posterior one more distant; left valve with a grooved anterior and thin posterior lamella-like cardinal, anterior lateral weak, posterior lateral represented by a triangular projection of the margin; the pallial sinus is highest posteriorly, rounded at the end and extends forward about four-fifths the length of the shell and is separated from the anterior adductor impression by a considerable distance, for over half its length along the base it is confluent with the pallial line.

A large right valve from Santa Inez Bay in the Gulf of California measures: length, 40.2 mm.; height, 29.6 mm.; convexity (one valve), 6.5 mm.; pallial sinus extends forward 31 mm. from the posterior end of the valve.

The exterior of fresh valves shows a brilliant iridescence of spectral colors due to the fine growth lines between the concentric ridges acting as a diffraction grating.

The specimens in the present collection show the differences pointed out by Pilsbry & Lowe between this species and *Tellina lyra*. They stated: "Related to *T. lyra* Hanley, but relatively longer, with the beaks less, only very slightly, turned forward, the dorsal margin in front of them less convex, and the concavity runnning to the posterior basal extremity wider." The concentric ribbing on *T. lyrica* is much finer and more closely spaced than that on *T. lyra*.

*Distribution*: This species was dredged in Santa Inez Bay in the Gulf of California, in 25-35 fathoms, off La Libertad, El Salvador, in 14 fathoms and in the Gulf of Chiriqui, Panama, in 35-40 fathoms, in mud and sandy mud. It also has been recorded as occurring in the Pliocene of Ecuador.

### Subgenus **Merisca** Dall.

### Key to the species of *Merisca*.

A. Interspaces with minute radial striae

a. Rostrum attenuated posteriorly; concentric lamellae about 1 per mm. *crystallina*

aa. Rostrum not attenuated posteriorly; concentric lamellae about 5 per mm. *reclusa*

B. Interspaces without radial striae *proclivis*

#### **Tellina (Merisca) crystallina** Spengler.

*Tellina crystallina* Chemnitz, Neues Syst. Conchyl.-Cab. von Martini-Chemnitz, Bd. 11, 1795, p. 210, pl. 199, figs. 1947, 1948. "Es ist diese Muschel an der Nordamericanischen Küste bey Newport auf Rhode-Island gefunden worden." (Spengler). —Spengler, *Skr. Nat. Selsk.* (Copenhagen), Vol. 4, No. 2, 1798, p. 113. "Fra Newport Long-Island." Ref. to Chemnitz, pl. 199, figs. 1947, 1948.—Wood, General Conch., 1815, p. 149. [No locality cited]. Ref. to Chemnitz, pl. 199, figs. 1947, 1948.—Hanley, Thes. Conch., Vol. 1, 1846, p. 270, pl. 57, fig. 43. "St. Elena, West Columbia."—Olsson, *Bull. Amer. Paleo.*, Vol. 9, No. 39, 1922, p. 421 (249), pl. 29 (26), fig. 10. Banana River, Costa Rica. Miocene. Also Recent.

*Tellina (Merisca) crystallina* Wood, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, pp. 293, 302, 311, pl. 2, fig. 10. Sullivans Island, South Carolina, to Cartagena, Colombia. Lower California to Panama.—M. Smith, Panamic Mar. Shells (Tropical Photogr. Lab., Winter Park, Florida), p. 64, fig. 834. Lower California to Guayaquil, Ecuador. Also West Indies.

*Tellina schrammi* Recluz, *Journ. de Conchyl.*, Vol. 4, December, 1853, p. 152, pl. 6, figs. 7, 8. . . "habite la rade de la Pointe-à-Pitre (Guadeloupe): elle a été draguée sur un fond vaseux au fond de cette rade."

*Type Locality*: Newport, Rhode Island.

*Range*: Scammon Lagoon, Lower California, to the Gulf of California and south to Guayaquil, Ecuador. Also Atlantic, from Charleston, South Carolina, to Cartagena Bay, Colombia.

*Collecting Stations*: Mexico: Tangola-Tangola Bay, on beach; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves, also on beach.

*Description*: Shell rather small, roundly trigonal, posteriorly rostrate, somewhat attenuated and with a sharp flexure, thin, white; sculpture of strong, raised distant, concentric ribs separated by much wider interspaces (about 1 mm. wide) although the spacing varies with various specimens, and where the lamellae cross the flexure they are V-shaped; the interspaces contain fine concentric striae (sometimes about 8) and faint radial striae; right posterior and left anterior cardinals grooved, lateral teeth in right valve well developed, in the left obsolete or nearly so; pallial sinus high behind then descending and sometimes touching the base of the anterior adductor impression, wholly confluent with the pallial line below.

The specimens in the present collection are

small but a large valve in the collections of the California Academy of Sciences, from Mazatlan, Mexico, measures: length, 23 mm.; height, 17.4 mm.; convexity (one valve), 3.4 mm.

Chemnitz originally described and illustrated *Tellina crystallina* and cited Spengler as the authority for the locality, Newport, Rhode Island. The International Committee on Zoological Nomenclature has recently ruled against acceptance of the specific names proposed by Chemnitz. Spengler next described the species. He referred to Chemnitz's description and illustrations and gave the same locality as Chemnitz. However, the species is not known with certainty to occur north of Charleston, South Carolina. One might venture the opinion that since Spengler was a citizen of Denmark, the type specimens secured by him originally might have come from the Danish West Indies.

Salisbury[45] recently stated that the east and west American shells referred to this species should be considered as separate species. So far as we have been able to determine, there is no reason to differ from Dall's[46] conclusion that "The specimens from the two oceans are absolutely similar, and differ no more than individuals from either sea among themselves." *Tellina schrammi* Recluz, described from the island of Guadeloupe in the West Indies, appears to be identical with *T. crystallina*.

*Tellina errati* Pilsbry & Johnson[47], described from the Miocene of Santo Domingo, is identical or a very similar form. Maury,[48] 1917, stated that fossils from Santo Domingo were identical with Recent shells found on the beach on that island.

*Tellina (Merisca) sancti-dominici* Maury,[49] also described from the Miocene of Santo Domingo, is a similar species. *Tellina martensi* Lynge,[50] described from the East Indies, was compared to *T. crystallina*, but the west American species is longer with a more rostrate form.

*Distribution*: A few specimens of this species were collected by the expedition on the beach at Tangola-Tangola, Mexico, and others were dredged in 12-13 fathoms at Corinto, Nicaragua. It also occurs from Miocene to Recent in the Caribbean region and has been recorded as occurring in the Pliocene of Ecuador and Pleistocene of Magdalena Bay, Lower California.

**Tellina (Merisca) proclivis** Hertlein & Strong, sp. nov.

Plate I, Figs. 6, 7, 14.

*Tellina declivis* Sowerby, Conch. Icon., Vol. 17, *Tellina*, March, 1868, species 261, pl. 44, fig. 261. "Hab.—?"—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 165 (under section *Merisca*). Catalina Island, California, to Panama.—Strong & Hertlein, Allan Hancock Pac. Exped., Vol. 2, No. 12, 1939, p. 184. Bahia Honda, and off Taboga Island, Panama.

Not *Tellina declivis* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 1, Vol. 7, 1834, p. 131. "Locality, Yorktown, Va." Tertiary. [Miocene].

*Tellina (Merisca) declivis* Sowerby, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 301. "Cerros Island, Lower California, to the Gulf of California."

*Type Locality*: Magdalena Bay, Lower California, Mexico.

*Range*: Cedros Island, Lower California, to Panama.

*Collecting Stations*: Mexico: 4 miles SSW. of Maldanado Point (192-D-1), 26 fathoms, mud; Port Guatulco (195-D-20), 23 fathoms, mud; Tangola-Tangola Bay (196-D-17), 23 fathoms, mud; Costa Rica: Port Parker (203-D-1, 3), 12-15 fathoms, sandy mud, crushed shell, shelly mud.

*Description*: Shell small, subtrigonal, white, beaks subcentral and elevated; anterior dorsal margin sloping, anteriorly rounded and inflated, posterior dorsal margin steeply sloping, the end pointed, wedge-shaped, subcompressed; a well-developed and sunken lunular area and long escutcheon present; right valve with a broad flexure, the left with a shallow radial depression followed by an angulation; sculpture of fine, regular, concentric lamellae, about 3 or 4 per millimeter on adult shells; hinge of right valve with two strong cardinals, the posterior one grooved, and two laterals, left valve with a strong grooved anterior and weaker posterior cardinal, the latter close to the margin, the posterior cardinal in each valve grooved, pallial sinus high in the middle then descending near to but not touching the anterior adductor impression, then bending posteriorly and for about half its length confluent with the pallial line. Dimensions of the type: length, 9 mm.; height, 7.8 mm.; convexity (both valves together), 4.8 mm.

Holotype (Calif. Acad. Sci. Paleo. Type Coll.), from Loc. 20299 (C.A.S.), Magdalena Bay, Lower California, Mexico; Charles R. Orcutt collector. Paratype, from station 196-D-17, Lat. 15°45′ N., Long. 96°05′34″ W., Tangola-Tangola Bay, Mexico, dredged in 23 fathoms, mud.

One of the largest valves in the present collection measures 9.3 mm. in length. A large right valve dredged about 5 miles west of Mazatlan, Mexico, by the Templeton

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[45] Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 83.

[46] Dall, W. H., *Proc. U. S. Nat. Mus.*, Vol. 23, 1900, p. 302.

[47] *Tellina (Merisca) errati* Pilsbry & Johnson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 69, May 5, 1917, p. 201. Santo Domingo, Oligocene [Miocene].—Pilsbry, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 73, Pt. 2, 1922, p. 425, pl. 41, fig. 7. [Figure of type].

[48] Maury, C. J., *Bull. Amer. Paleo.*, Vol. 5, No. 29, 1917, pp. 387 (223)-388 (224), pl. 64 (38), fig. 4.

[49] *Tellina (Merisca) sancti-dominici* Maury, *Bull. Amer. Paleo.*, Vol. 5, No. 29, Pt. 1, April 7, 1917, p. 388 (244), pl. 64 (38), fig. 11. "Bluff 3, Cercado de Mao." Santo Domingo, Miocene.

[50] *Tellina (Merisca) martensi* Lynge, *Kgl. Dansk. Vidensk. Skr.*, Ser. 7, Nat. og Math., Bd. 5, 1909, p. 195, pl. 3, figs. 40-42. "South of Koh Kut, 17-20 fathoms, mud (½). Gulf of Siam. Singapore, 2-3 fathoms, coral reef; 5/2."

Crocker Expedition of the California Academy of Sciences in 1932, measures: length, 11.4 mm.; height, 9.8 mm.; convexity (one valve, 3 mm.

The use of the combination of names, *Tellina declivis* by Conrad, 1834, makes it necessary to propose a new name which is based on a new type specimen for the west American shell described under that name by Sowerby in 1868 which is here named *Tellina proclivis*.

The shell of *Tellina proclivis* differs from that of *T. reclusa* in the more steeply sloping dorsal margins, in lacking radial sculpture, in that the pallial sinus does not touch the anterior adductor impression and along the base it is confluent with the pallial line for only about one-half its length. It differs from *T. meropsis* in the more steeply sloping dorsal margins, more pointed posterior end and in the narrower, radially depressed area posteriorly.

*Distribution*: Specimens of this species, mostly single valves, were dredged by the expedition off western Mexico and Costa Rica in 12-26 fathoms, mostly on a mud bottom. Dall[51] cited this species as occurring north to Catalina Island, California, but Burch[52] indicated that it is questionable whether it is a member of the fauna of California.

### *Tellina (Merisca) reclusa* Dall.

*Tellina (Merisca) reclusa* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 301, 315, pl. 3, fig. 2. "Types.—No. 105513, U. S. N. M., from San Ignacio Lagoon, Lower California, Hemphill. Also off Lower California, in lat. 30° 28′, by the U. S. Fish Commission, at Station 3019, in 14 fathoms, Gulf of California."

*Tellina reclusa* Dall, E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.*, Vol. 1, No. 4, 1936, p. 145. Magdalena Bay and San Ignacio Lagoon, Lower California, Pleistocene. Recent from San Ignacio Lagoon to the Gulf of California.

*Type Locality*: San Ignacio Lagoon, Lower California.

*Range*: San Ignacio Lagoon, Lower California, to the Gulf of California and south to Bahia Honda, Panama.

*Collecting Stations*: Mexico: Arena Bank, Gulf of California (136-D-18, 21, 22), 40-45 fathoms, mud; Santa Inez Bay, Gulf of California (142-D-3; 145-D-1, 3), 4-40 fathoms, sand, weed; Port Guatulco (195-D-2, 3), 3-3.5 fathoms, sand, crushed shell, Tangola-Tangola Bay (196-D-14-15), 5 fathoms, crushed shell; Nicaragua: Corinto (200-D-8, 9), 6-6.6 fathoms, mangrove leaves, also on beach.

*Description*: Shell small, moderately convex, subtrigonal, posteriorly wedge-shaped and flexed, the posterior end keeled dorsally; sculpture of fine, close (about 5 per mm.), little elevated, sharp, concentric lamellae which are separated by wider interspaces which are faintly, radiately striated; lunular area smooth, escutcheon long, narrow, deep; hinge normal for the subgenus; pallial sinus high behind then descending and usually, although not always, touching the base of the anterior adductor impression and wholly confluent with the pallial line below.

A specimen from Tangola-Tangola Bay, Mexico, measures: length, 20 mm.; height, 15.5 mm.; convexity (one valve), 3.6 mm.

Dall stated that "this species is notable for the rasp-like quality of its surface to the touch."

Compared to *Tellina proclivis* the shell of *T. reclusa* is longer in proportion to the height, the dorsal margins slope less steeply and the interspaces are ornamented by fine radial sculpture. The shell of *T. reclusa* is more elongate in outline but the posterior end is less attenuated and flexed and the concentric sculpture is more closely spaced than that of *T. crystallina*. The coarser sculpture and the fact that the pallial sinus usually touches the anterior adductor impression are features separating *T. reclusa* from *T. meropsis* Dall[53].

*Tellina (Merisca) lintea* Turton, which occurs in the Caribbean region from Florida to Brazil, is very similar to *T. reclusa*. *Pristipagia gemonia* Iredale,[54] an Australian species, also is a somewhat similar shell.

*Distribution*: This species was collected by the expeditions from Santa Inez Bay in the Gulf of California, to Corinto, Nicaragua, on the beach and dredged at depths of 3-45 fathoms. It is also known to occur in the Pleistocene of Lower California.

## Subgenus *Scissula* Dall.

### Key to the species of *Scissula*.

A. Shell large, length exceeding 25 mm.
  a. Posterior end obliquely truncated; white or tinged with brown ... *cognata*
  aa. Posterior end tapering and roundly pointed; pale rose color ..... *nicoyana*

B. Shell small, length not exceeding 25 mm.; very thin, glassy
  a. Oblique striae widely spaced, coarse, very oblique ..... *virgo*
  aa. Oblique striae closer, finer, less oblique and approaching lines of growth *varilineata*[55]

[55] Not represented in the present collection.

### *Tellina (Scissula) cognata* C. B. Adams.

*Tellina cognata* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 503, 545 (separate pp. 279, 321). "Habitat. —Panama."

[51] *Arcopagia declivis* Sowerby, Dall, *U. S. Nat. Mus., Bull. 112*, 1921, p. 45 (under section *Merisca*). Catalina Island, California, to Panama.

[52] Burch, J. Q., *Min. Conch. Club South Calif.*, No. 45,

[53] *Tellina (Moerella) meropsis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 317, pl. 3, fig. 1. "San Diego, California."

[54] *Pristipagia gemonia* Iredale, *Rec. Australian Mus.*, Vol. 19, No. 5, April 7, 1936, p. 281, pl. 21, fig. 6. "Habitat.

*Psammobia casta* Reeve, Conch. Icon., Vol. 10, *Psammobia*, June, 1857, species 55, pl. 8, fig. 55. "Hab. Guatemala."

Not *Tellina casta* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 63. "Hab. Singapore; sandy mud."

*Tellina tenuilineatus* Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, October, 1930, p. 262, pl. 5, fig. 33. "Brought up by marine dredge from depths varying from 10. ft. to 40. ft. in the mud at the mouth of the Rio Grande near La Boca about one mile from the mainland in Panama Bay." "Horizon: Probably Gatun formation." According to Pilsbry this record is based upon "Two pieces of a left valve of '*Tellina*' *cognata* C. B. Ad. Compared with Adams' type" (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 431).

*Type Locality*: Panama.

*Range*: Mazatlan, Mexico, to Panama.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Monypenny Point, Gulf of Fonseca (199-D-4, 5, 6), 4-7 fathoms, mud; Costa Rica: 13 miles S. × E. of Judas Point (214-D-1), 42 fathoms, mud, shell; Panama: Gulf of Chiriqui (221-D-1-5), 35-40 fathoms, sandy mud.

*Description*: Shell oblong, anterior end obliquely rounded, posterior end obliquely truncated, gaping, a depressed posterior area is delimited by a rounded umbonal angulation, white or with a reddish or pale brownish tinge; sculpture consists of minute unequal radiating striae and concentric grooved striae which cross the lines of growth obliquely and become weak or absent on the posterior third of the shell; lateral teeth obsolete; pallial sinus highest posteriorly then descending gently and extending anteriorly for a little more than three-fourths the length of the shell but well separated from the anterior adductor impression; basally, for about one-half its length, it is confluent with the pallial line.

A specimen from the Gulf of Fonseca, in the present collection, measures: length, 45.3 mm.; height, 30 mm.; convexity (both valves together), 13.5 mm.; pallial sinus extends forward 36.4 mm. from the posterior end of the shell. A large left valve dredged in the Gulf of Chiriqui, Panama, measures: length, 49.5 mm.; height, 32 mm.; convexity (one valve), 7.5 mm.

This species is unlike any other along the Pacific Coast of the Americas. It bears only a general resemblance to the east American species *T. similis* Sowerby.

The present species appears to be referable to the subgenus *Scissula* Dall, 1900, type *Tellina decora* Say, rather than to other supraspecific groups in which the shell bears oblique striations such as *Scissulina* Dall, 1924, type, *T. dispar* Conrad; *Jactellina* Iredale, 1929, type, *T. obliquaria* Deshayes; *Obtellina* Iredale, 1929, type, *T. bougei* Sowerby; and *Loxoglypta* Dall, Bartsch & Rehder, 1938, type, *T. obliquilineata* Conrad.

*Distribution*: This species was dredged by the expedition from Guatemala to Panama in 4-42 fathoms. It occurred rather abundantly off Champerico, Guatemala, in 14 fathoms, and in the Gulf of Chiriqui, Panama, in 35-40 fathoms, mostly on a muddy bottom. It also has been recorded as occurring in the Pliocene of Ecuador.

**Tellina (Scissula) nicoyana** Hertlein & Strong, sp. nov.

Plate I, Figs. 23, 24, 25, 26.

Shell elongately ovate, thin, gently inflated, nearly equilateral, color, pale rose; anterior dorsal margin slightly rounded, gently sloping anteriorly then rounding abruptly to the elliptically rounded anterior end which merges into the broadly rounded ventral margin; posterior end tapering, roundly pointed; the posterior dorsal margin slopes gently from the beaks with a convexity in the middle portion; the ornamentation consists of fine concentric lines of growth; these are crossed by oblique striae which begin on the anterior end and continue for about two-thirds the length of the shell but are absent on the posterior end where there are a few vague submicroscopic radiating striae; hinge of right valve with two grooved cardinals and, close by, an anterior lateral, and distally a posterior socket below which is a weak lateral; left valve with a grooved anterior cardinal and a thin lamella-like posterior cardinal, also a short anterior lateral or projection of the nymph and a faint posterior lateral; pallial sinus extending about four-fifths the length of the shell and separated from the anterior adductor impression by a considerable distance, high and rounded beneath the beaks then sloping and broadly undulating downward then turning abruptly downward to the pallial line with which it is confluent below; interior beautifully pale yellowish-rose and with faint submicroscopic radiating striae. Length, 34.4 mm.; height, 19 mm.; convexity (both valves together), 7.8 mm.; pallial sinus extends forward about 27 mm. from the posterior end of the shell.

Holotype and paratypes (Calif. Acad. Sci. Paleo. Type Coll.), dredged in Ballena Bay, Gulf of Nicoya, Costa Rica; also dredged in the same vicinity at Station 213-D-11, 17, in Lat. 9° 44′ 52″ to 9° 42′ 00″ N., Long. 84° 51′ 25″ to 84° 56′ 00″ W., in 35 fathoms, mud.

This beautiful species appears to be distinct from any described shell. It apparently has some characters in common with *Tellina delicatula* Deshayes[56], the type of which has never been illustrated, but differs in that the shell is nearly equilateral, rather than strongly inequilateral, and the hinge is quite different from that described by Deshayes. It also lacks the dark irregular lines crossing the oblique striae on that species mentioned

[56] *Tellina delicatula* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 363. "Hab. Mazatlan. Coll. Cuming."—Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 1, 1878, p. 290. Coast of Mazatlan.

by Carpenter[57]. It is interesting to note that Maury has described *Tellina* (*Scissula*) *cercadica*[58] from the Miocene of Santo Domingo, which species, she stated, is very similar to a Recent shell from Panama Bay in the Newcomb collection which was labeled *Tellina delicatula* Deshayes. The Miocene shell illustrated by Maury is not at all similar to the present species but is more similar to *Tellina* (*Scissula*) *cognata* C. B. Adams from Panama.

**Tellina (Scissula) virgo** Hanley.

*Tellina virgo* Hanley, *Proc. Zool. Soc. London,* December, 1844, p. 143. "Hab. —? Mus. Cuming." "Allied to the *Iris* of Say, but much larger." —Hanley, Thes. Conch., Vol 1, 1846, p. 284, pl. 57, fig. 42. "Chiriqui, West Columbia." —Sowerby, Conch. Icon., Vol. 17, *Tellina,* 1867, species 207, pl. 37, fig. 207. "Hab. Chiriqui, West Indies." —Pilsbry & Olsson, *Nautilus,* Vol. 56, No. 3, January, 1943, p. 79 (in text), pl. 8, fig. 5. Panama and west coast of northern South America to Puerto Pizarro, Peru.

*Tellina* (*Fabulina*) *virgo* Hanley, Salisbury, *Proc. Malacol. Soc. London,* Vol. 21, Pt. 2, July, 1934, p. 91, pl. 13, figs. 5 and 6. [Illustrations of holotype and paratype].

*Type Locality*: Chiriqui, west Panama (here designated as type locality). No locality cited originally.

*Range*: Magdalena Bay to the Gulf of California and south to Puerto Pizarro, Peru.

*Collecting Stations*: Nicaragua: Corinto (200-D-11-13, 15), 1-8 fathoms, mangrove leaves, also on beach.

*Description*: Shell small, ovately elongate, very thin, glassy, transparent, obtusely angulated posteriorly, colored pink or white; sculpture consists of fine striae which cross the shell obliquely but are absent on the posterior area; the pallial sinus projects anteriorly about four-fifths the length of the shell but does not quite touch the anterior adductor impression, along the base it is confluent with the pallial line.

One of the largest valves collected on the beach at Corinto, Nicaragua, measures: length, 20.2 mm.; height, 12 mm.; convexity (one valve), 2 mm.

The spacing of the oblique lines on this shell seems to vary somewhat but on the specimens which we have observed these lines are always more widely spaced and cross the shell at a greater inclination than those of the similar *Tellina* (*Scissula*) *varilineata* Pilsbry & Olsson[59].

*Distribution*: This species was collected by the expedition only at Corinto, Nicaragua, on the beach and dredged in 1 to 8 fathoms.

[57] Carpenter, P. P., Cat. Mazatlan Shells, September, 1855, p. 37.

[58] *Tellina* (*Scissula*) *cercadica* Maury, *Bull. Amer. Paleo.*, Vol. 5, No. 29, Pt. 1, April 7, 1917, p. 388 (224), pl. 64 (38), fig. 9. "Bluff 3, Cercado de Mao." Santo Domingo, Miocene.

[59] *Tellina* (*Scissula*) *varilineata* Pilsbry & Olsson, *Nautilus*, Vol. 56, No. 3, January, 1943, p. 79, pl. 8, fig. 6. Type, "from Puerto Bucaro, Province of Los Santos, Panama." Also ranges south to Puerto Pizarro, Province of Tumbez, Peru.

Subgenus **Phyllodina** Dall.

**Tellina (Phyllodina) pristiphora** Dall.

*Tellina* (*Phyllodina*) *pristiphora* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 302, 316, pl. 4, fig. 14. "Dredged near La Paz, Lower California, in 26½ fathoms."

*Tellina pristiphora* Dall, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 84, 1932, p. 132. Dredged in 20 fathoms, Manzanillo; Acapulco, Mexico.

*Type Locality*: Near La Paz, Lower California, in 26½ fathoms.

*Range*: Santa Inez Bay, Gulf of California, to Puntarenas, Costa Rica.

*Collecting Stations*: Mexico: Arena Bank, Gulf of California (136-D-4, 7, 9, 15, 18, 20-22, 28, 32), 40-85 fathoms, mud, crushed shell, muddy sand, sand; Santa Inez Bay (146-D-1), 35 fathoms, mud, crushed shell; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Port Guatulco (195-D-21), 18 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly sand.

*Description*: Shell of medium size, ovate, compressed, nearly equilateral, beaks low, anterior end rounded, posterior dorsal margin sloping, the end blunt, surface yellowish-white, somewhat chalky; sculpture consists of evenly spaced concentric lamellae which are separated by wider and finely concentrically striated interspaces, the lamellae are somewhat obsolete medially; on the posterior area, which on the right valve is set off by an angulation and on the left valve by a groove, the lamellae develop small squarish or rounded elevated foliations, along the anterior dorsal margin similar foliations present a serrated character; lunule and escutcheon elongate; two cardinal teeth in each valve, the right posterior and left anterior ones grooved, two large laterals in the right valve and two small ones in the left, the anterior ones closest to the cardinals; pallial sinus highest behind, then tapering, the end pointed, extending toward the anterior adductor impression for more than one-half the length of the shell, free and ascending from the pallial line except for a short distance posteriorly; interior white and in large specimens yellowish which becomes pale salmon in the anterior dorsal area.

A large specimen dredged on Arena Bank in the southern portion of the Gulf of California measures: length, 35.8 mm.; height, 23 mm.; convexity (both valves together), 10.2 mm.; pallial sinus extends forward 21.5 mm. from the posterior end of the shell.

*Tellina fluctigera* Dall[60], described from the Gulf of Panama, the type of which has not been illustrated, appears to be a very similar form.

*Tellina dodona* Dall and *T. leptalea* Gardner are representative of the subgenus *Phyllodina* in the Miocene of Florida.

[60] *Tellina* (*Phyllodina*) *fluctigera* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 419. Dredged "in the Gulf of Panama, in 182 fathoms, mud, bottom temperature 54°.1 F."

*Distribution*: Specimens of *Tellina pristiphora* were dredged from Santa Inez Bay, in the Gulf of California, to Port Parker, Costa Rica, in 12-85 fathoms. The present record of occurrence at Costa Rica is an extension south of the known range of this species.

### Subgenus **Phyllodella** Hertlein & Strong, subgen. nov.

Shell elongate, compressed, moderately thin, equilateral, both sides sloping nearly equally, anterior end rounded, posterior end roundly obliquely truncated, a posterior area is set off by a weak posterior umbonal angulation; sculpture consists of fine close concentric threads which are crossed by fine radial striae; on the posterior area the concentric sculpture becomes squamose with fine plate-like scales; right valve with two grooved cardinals, a close anterior lateral and a small distant posterior lateral; left valve with a grooved anterior cardinal, a thin posterior cardinal and a weak anterior lateral, no posterior lateral; pallial sinus long, almost touching the anterior adductor impression, along the base wholly confluent with the pallial line.

The character of the hinge, the pallial sinus, and concentric sculpture anterior to the posterior angulation in this subgenus are similar to those of *Eurytellina*. The character of the posterior area, ornamented with squamose foliations, resembles that of *Phyllodina* Dall.

#### **Tellina (Phyllodella) insculpta** Hanley.

*Tellina insculpta* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 70. "Hab. Chiriqui, West Columbia; sandy mud, three fathoms." —Hanley, Thes. Conch. Vol. 1, 1846, p. 289, pl. 60, fig. 136. "Chiriqui, W. Columbia." —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 208, pl. 37, fig. 208. "Hab. Chiriqui, West Columbia."

*Type Locality*: Chiriqui, west Panama, in three fathoms, sandy mud.

*Range*: Champerico, Guatemala, to Santa Elena Bay, Ecuador.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud.

*Description*: Shell elongate, compressed, thin, white, equilateral, dorsal margins sloping, anterior end rounded, posterior end angulated; sculpture of fine, close, equidistant, concentric ribs (about 4 per mm.), both ribs and interspaces are crossed by fine submicroscopic radiating striae; posterior area set off by a weak angulation and on this area the surface is roughened by small scales or interrupted delicate lamellae; right valve with two grooved cardinals and an anterior lateral so closely situated near the beaks as to resemble a cardinal, and a small posterior lateral; left valve with a grooved anterior cardinal, a thin posterior cardinal and a faint anterior lateral; pallial sinus rather high behind then descending, end blunt and almost, but not quite, touching the posterior basal margin of the anterior adductor impression, along the base it is confluent with the pallial line.

The largest specimen in the collection measures: length, 33.6 mm.; height, 18.3 mm.; convexity (both valves together), 5.8 mm.

The only other shell described from west American waters that bears much resemblance to this species appears to be *Tellina* (*Phyllodina*) *fluctigera* Dall, the type of which has not been illustrated. According to Dall's description the concentric sculpture of his species is more widely spaced (about 2 lamellae per mm. whereas there are about 4 per mm. in the present species) and the pallial sinus is entirely free from the pallial line rather than confluent with it.

*Distribution*: Specimens of *Tellina insculpta* were dredged by the expedition west of Champerico, Guatemala, in 14 fathoms, and at La Libertad, El Salvador, in 13 fathoms, on a muddy bottom. A small specimen of this species in the collections of the California Academy of Sciences was collected by Woodbridge Williams in Santa Elena Bay, Ecuador. These records extend the known range of the species both to the north and to the south.

### Subgenus **Elliptotellina** Cossmann.

#### **Tellina (Elliptotellina) pacifica** Dall.

*Tellina* (*Elliptotellina*) *pacifica* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, pp. 302, 316, pl. 3, fig. 9. . . . "dredged in Panama Bay, in 18 fathoms, sand."

*Type Locality*: Panama Bay, in 18 fathoms, sand.

*Range*: Santa Inez Bay, in the Gulf of California, to the Bay of Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Lower California, in the Gulf of California (145-D-1-3), 4-13 fathoms, sand; Manzanillo (184-D-2), 30 fathoms, gravelly sand; Port Guatulco (195-D-9, 19), 7-17 fathoms, gr. mud, gr. sand, crushed shell; Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell.

*Description*: Shell small, oval, both ends rounded, the anterior the longer, moderately convex, yellowish-white with a rose colored spot near each end of the hinge margin; sculpture of fine concentric grooves separated by wider interspaces, these on the posterior half (and sometimes faintly to the anterior third) of the shell are crossed by deep, angular, radial grooves which serrate the posterior ventral margin and between which are narrow interspaces; hinge of right valve with two cardinals, the anterior one a large subtriangular mass and the posterior one smaller and faintly grooved, two laterals present; left valve with two cardinals, the anterior one grooved, the laterals obsolete; pallial sinus ascending, extending anteriorly about one-half or more the length of the shell, rounded at the end and, except for a short

distance posteriorly, free from the pallial line.

A specimen from Tangola-Tangola Bay, Mexico, measures approximately: length, 7.8 mm.; height, 4.4 mm.; convexity (both valves together), 2.5 mm. A left valve from Port Guatulco, Mexico, measures 8.2 mm. in length.

This species differs from *Tellina americana* Dall, 1900, a similar east American species, in that the radial sculpture is stronger and is present farther anteriorly, the pallial sinus is longer and the color is said to be somewhat brighter.

*Tellina cymobia* Woodring[61], described from the Miocene of Jamaica, is a very similar species.

*Distribution*: The discovery of the occurrence of *Tellina pacifica* in Santa Inez Bay in the Gulf of California is a long extension north of the known range of the species.

Genus **Tellidora** Mörch in H. & A. Adams.

**Tellidora burneti** Broderip & Sowerby.

*Tellina burneti* Broderip & Sowerby, *Zool. Jour.*, Vol. 4, No. 15, January, 1829, p. 362, pl. 9, fig. 2. "Hab. ad Mazatlan, in Aestuario." "Found in the Estuary of Mazatlan, among the shoals of large Pinnae which are left dry at low water." —Hanley, Thes. Conch., Vol. 1, 1846, p. 271, pl. 58, fig. 99. "Salango, W. Columbia." —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 199, pl. 35, figs. 199a, 199b. West Colombia. —M. Smith, Panamic Shells (Trop. Photogr. Lab., Winter Park, Florida), 1944, p. 65, fig. 843. Lower California to Ecuador.

*Type Locality*: Mazatlan, Mexico, in the estuary among shoals of large Pinnae at low water.

*Range*: Soledad, Lower California, to the Gulf of California and south to Salango, Ecuador.

*Collecting Stations*: Mexico: Port Guatulco (195-D-17), 6 fathoms, sand; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Corinto, beach.

*Description*: Triangular, rather thin, inequivalve, subequilateral, compressed, subnacreous, white; the convex valve with obsolete distant dilated concentric grooves, which are most visible in front and towards the elevated acute and curving beaks (one of which projects over the other); the flat valve with the elevated fine rather irregular and close concentric striae, which become obsolete posteriorly; ventral edge arcuated; dorsal edges strongly sloping on either side, and armed with large tooth-like projections, the front one greatly incurved, the hinder nearly straight; ligament minute; dorsal slopes excavated; fold and flexure distinct; lateral teeth distinct, rather remote, and subequidistant. (Hanley, Thes. Conch., Vol. 1, 1846, p. 271).

The pallial sinus is rather high and projects anteriorly more than half the length of the shell.

A large valve in the present collection from the Gulf of Fonseca, measures: length, 49 mm.; height, 40.5 mm.; convexity (one valve), approximately 3.4 mm.

There is some variation in the concentric sculpture of this species but the shape and ornamentation are so characteristic that it cannot be confused with any other west American shell.

*Tellidora cristata* Récluz[62] is a similar species which occurs from Miocene to Recent in the Caribbean region. *Tellidora* (*Tellipiura*) *peruana* Olsson, 1944, has been described from the Cretaceous of Peru.

*Distribution*: This species was collected by the expedition off west Mexico, in the Gulf of Fonseca off El Salvador and at Corinto, Nicaragua. It also has been recorded as occurring in the Pleistocene at Magdalena Bay, Lower California, and Panama.

Genus **Macoma** Leach.

KEY TO THE SUBGENERA OF *Macoma*.

A. Shell subtrigonal, beaks subcentral
  a. Shell ornamented with slightly oblique corrugations; small; thin....*Cymatoica*
  aa. Shell ornamented with concentric striae only .....*Macoma* s.s.
B. Shell elongate, beaks posteriorly situated; posterior end much the shorter
  a. Resilium internal and shorter than the ligament .....*Psammotreta*
  aa. Resilium external and about as long as the ligament
    b. Posterior area granulated *Macoploma*
    bb. Posterior area not granulated *Psammacoma*

Subgenus **Macoma** s.s.

**Macoma (Macoma) nasuta** Conrad.

*Tellina nasuta* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Ser. 1, Vol. 7, 1837, p. 258. "Inhabits coast of California near Sta. Diego."

*Macoma nasuta* Conrad, I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 174, pl. 45, figs. 1a, 1b, 1c, 1d. Kodiak Island and Cook Inlet, Alaska, to Scammon Lagoon, Lower California. Also Miocene, Pliocene and Pleistocene of California. —Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 365, pl. 20, figs. 11a, 11b. Earlier records cited. ? Oligocene and Miocene to Recent.

[61] *Tellina* (*Elliptotellina*) *cymobia* Woodring, *Carnegie Inst. Washington, Publ.* 366, May 20, 1925, p. 174, pl. 24, figs. 14-16. Bowden, Jamaica, Miocene.

[62] *Lucina cristata* Récluz, *Rev. Zool., Soc. Cuvierienne*, 1842, p. 270. "Hab.: —Trouvée sur le banc de Campeche par M. Cosmao, commandant la station navale du Mexique." —Récluz, *Mag. de Zool.* (par Guérin-Méneville), 1843, Moll., pl. 60, p. 1, figs. 1-5. Original locality cited.

*Tellina cristata* Récluz, Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1868, species 291, pl. 49, figs. 291a, 291b. "Hab. —?" —M. Smith, East Coast Mar. Shells (Edwards Bros., Ann Arbor, Michigan), 1937, p. 60, pl. 54, figs. 6a, 6b. West Florida to Trinidad, West Indies.

*Type Locality*: Coast near San Diego, California.

*Range*: Kodiak Island and Cook's Inlet, Alaska, to Cape San Lucas, Lower California.

*Collecting Station*: Mexico: Cape San Lucas, Lower California.

*Description*: A single right valve of this well known strongly flexed shell, measuring 81 mm. in length and 42.8 mm. in height, was taken by the expedition at Cape San Lucas, Lower California.

The present specimen might be referable to *Macoma kelseyi* but it appears to be intermediate in characters between that form and *M. nasuta*. Dall described *Macoma kelseyi*[63] from the "Pleistocene" of San Diego, California.

It was said to differ from *M. nasuta* by its greater size, thicker, flatter shell and in that the pallial sinus in the right valve bends posteriorly before coalescing with the pallial line rather than joining it at a right angle. Study of a series of specimens of *Macoma nasuta* and of *M. kelseyi* reveals that there is some variation in the pallial sinus and it may be open to question whether *Macoma kelseyi* is a distinct species, subspecies, or merely a very large *M. nasuta*.

*Distribution*: The discovery of the occurrence of *Macoma nasuta* at Cape San Lucas, Lower California, is an extension south of the known range of the species. It also is known to occur as a fossil in California from Oligocene or Miocene to Recent.

### Subgenus **Cymatoica** Dall.

#### **Macoma (Cymatoica) undulata** Hanley.

*Tellina undulata* Hanley, *Proc. Zool. Soc. London*, September, 1844, p. 72. "Hab. St. Elena, West Columbia; sandy mud, six fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 310, pl. 59, figs. 107, 107*. "St. Elena, West Columbia." —Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 119, pl. 23, figs. 119a, 119b. "St. Elena, West Columbia."

*Cymatoica occidentalis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 12, No. 773, 1889 (issued March 7, 1890), p. 272, pl. 10, fig. 11. Dredged ". . . in latitude 24° 18′ N., longitude 110° 22′ W., off the coast of Lower California, in 26½ fathoms, fine sandy mud."

*Tellina* (*Cymatoica*) *undulata* Hanley, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 309. "Gulf of California, south to St. Elena, West Colombia."

*Type Locality*: Santa Elena, Ecuador, in 6 fathoms, sandy mud.

*Range*: Off the west coast of Lower California in Lat. 24° 18′ N., Long. 110° 22′ W., to the Gulf of California and south to Santa Elena, Ecuador.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand; Port Guatulco (195-D-19, 20), 17-21 fathoms, gr. mud, crushed shell, mud; Santa Cruz Bay (195-D-21), 18 fathoms, mud; Tangola-Tangola Bay (196-D-6, 7), 6-7 fathoms, sand, crushed shell; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud.

*Description*: Shell small, thin, oblong, beaks subcentral, bluntly pointed and flexed to the right posteriorly, ornamented with small, rounded, undulating riblets which do not coincide with the incremental lines of growth except partially so on the posterior fold.

A right valve from the Gulf of Fonseca, measures: length, 16.4 mm.; height, 9 mm.; convexity (one valve), 2.6 mm.

*Macoma orientalis* Dall[64], described from the Antilles, is a very similar species.

*Distribution*: Specimens of this species were dredged from the Gulf of California to Costa Rica, in 4 to 21 fathoms.

### Subgenus **Psammacoma** Dall.

KEY TO THE SPECIES OF *Psammacoma*.

A. Shell moderately thick; telliniform ..... *lamprolenca*

B. Shell thin; sometimes iridescent

  a. Posterior end narrow; length usually not exceeding 35 mm.

    b. Very narrow and thin ..... *panamensis*

    bb. Higher and thicker ..... *spectri*

  aa. Posterior end wide; length usually exceeding 35 mm. ..... *elongata*

#### **Macoma (Psammacoma) elongata** Hanley.

*Tellina elongata* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 144. "Hab. Chiquiqui [Chiriqui], West Columbia; in sand at three fathoms."—Hanley, Thes. Conch., Vol. 1, 1846, p. 302, pl. 62, fig. 199. "Chiriqui, West Columbia."—Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 137, pl. 25, fig. 137. "Hab. Chiriqui, West Columbia."

*Type Locality*: Chiriqui, Panama, in 3 fathoms, sand.

*Range*: Lower California (Lat. 30° 36′ N.) to Panama (Dall). Caribbean region (Dautzenberg).

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-21), 18 fathoms, mud; Acapulco (189-D-4), 28 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; La Union (199-D-8-10, 12-14, 22), 3-6 fathoms, mud, mangrove leaves; Nicaragua: Monypenny Point (199-D-2-6), 4-7 fathoms, mud; Costa Rica: Cedro Island, Gulf of Nicoya (213-D-1,10), 8-10 fathoms, mud; 14 miles S. × E. of Judas Point (214-D-1, 4), 42-61 fathoms, mud, shell, rocks.

*Description*: Shell elongate, thin, smooth,

[63] *Macoma kelseyi* Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, December, 1900, p. 1052, pl. 49, fig. 7. "Pleistocene of San Diego, California, obtained in the City Park by Dr. R. E. C. Stearns." According to Dr. W. P. Woodring (oral communication), the type of this species came from Pliocene beds.

[64] *Cymatoica orientalis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 12, 1889, No. 773, (issued March 7, 1890), p. 273, pl. 10, fig. 12. "Hab.—Samana Bay, Santo Domingo, in 16 fathoms, mud". . . . Also found at the same depth at Cardenas, Cuba.

white, sometimes iridescent outside, white within; anterior end rounded, posterior end produced and bluntly truncated; a submedian radial, depressed area present on the ventral half of the shell; ornamented with fine concentric lines of growth which are coarser along the posterior dorsal area, and along the posterior umbonal ridge there are faint irregular oblique striations that do not coincide with the lines of growth; hinge with two cardinals in each valve (on a large specimen the right anterior one sometimes somewhat roughened anteriorly), the posterior tooth slightly cleft, the left anterior cardinal slightly cleft, sometimes slightly indented at the base, on some specimens there are grooves along the margin back of the posterior tooth; pallial sinus higher behind and rounded in front, projecting forward about two-thirds the length of the shell and along the base for about half its length confluent with the pallial line.

A specimen dredged southwest of Maldanado Point, Mexico, measures approximately: length, 47.4 mm.; height, 25.5 mm.; convexity (both valves together), 13 mm.; pallial sinus extends forward 30 mm. from the posterior end of shell.

*Tellina lamproleuca* Pilsbry & Lowe is a somewhat similar species but the median depressed area is less developed, the shell is thicker and more telliniform and the posterior end is generally narrower.

*Macoma gatunensis* Toula, 1908, described from the Miocene Gatun beds at Panama, is very similar but is more excavated beneath the beaks. The shell illustrated by Olsson[65] under the name of *Macoma guatunensis* Toula appears to be very similar to the present species; in fact Olsson mentioned that he could detect no differences between the fossil form and Recent specimens of *M. elongata*. *Macoma falconensis* H. K. Hodson, described from the Miocene of Venezuela, also is a somewhat similar form as is *Macoma hosfordensis* Mansfield[66] which was described from the upper Miocene of Florida.

The posterior area of *Macoma elongata* is smooth in comparison to somewhat similar species assigned to *Macoploma* Pilsbry & Olsson in which the posterior area is ornamented with granules.

*Distribution*: Specimens of *Macoma elongata* were dredged by the expedition from off western Mexico to Costa Rica, in 3 to 61 fathoms, mostly on a muddy bottom. Dautzenberg[67] cited this species as occurring at the island of St. Lucie in the West Indies and in the Gulf of Paria and Gulf of Maracaibo, Venezuela. We have not seen specimens from east American waters.

[65] Olsson, A. A., *Bull. Amer. Paleo.*, Vol. 5, No. 39, Pt. 2, June 21, 1922, pl. 29 (26), fig. 13. Banana River, Costa Rica. Miocene.

[66] *Macoma (Psammacoma) hosfordensis* Mansfield, *Florida Geol. Surv., Bull. 8*, 1932, p. 142, pl. 30, figs. 6, 10, 12, 13. "Type locality: Station 3671, 2 miles north of Hosford, Liberty County, Fla." Choctawhatchee, upper Miocene.

[67] Dautzenberg P., *Mem. Zool. Soc. France*, Vol 13, 1900, p. 263.

**Macoma (Psammacoma) lamproleuca** Pilsbry & Lowe.

*Tellina lamproleuca* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 93, pl. 11, figs. 6 and 7. "Corinto, Nicaragua." Also Panama.

*Macoma parthenopa* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 144, pl. 11, figs. 6 and 7. "Corinto," type. Also Panama.

*Macoma lamproleuca* Pilsbry & Lowe, Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, 1941, p. 69. Jama formation, Puerto Jama, and Canoa formation, Punta Blanca, Ecuador, Pliocene. Also Recent from Panama to Zorritos, Peru.

*Type Locality*: Corinto, Nicaragua.

*Range*: Santa Inez Bay, Gulf of California, to Zorritos, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (142-D-4), 40-50 fathoms, sand; Guatemala: 7 miles west of Champerico (197-D-1, 2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1, 2), 13-14 fathoms, mud; Meanguera Island (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell elongate, telliniform, fairly thick, white under a buff periostracum, somewhat inequilateral, the anterior end the longer, dorsal margins sloping and nearly straight, anterior end broadly rounded, posterior end bluntly truncated; surface ornamented with irregular lines of growth and wrinkles, stronger on the posterior area; sometimes in the right sometimes in the left valve the posterior area bears a median radial depression; a medial flattening from the umbos to the ventral margin often present; lunular area lanceolate and concave; hinge with two cardinals in each valve, the right posterior and left anterior ones bifid, no laterals present; the pallial sinus extends about four-sevenths the length of the shell, it is usually higher in the middle, rounded at the end and joins the pallial line at an acute angle and for a little over half its length is confluent with the pallial line.

The largest specimen in the present collection, a left valve, measures: length, 72.8 mm.; height, 40.5 mm.; convexity (one valve), 10.5 mm.; pallial sinus extends forward 41 mm. from posterior end of shell.

The shell of this species is similar to that of *Macoma elongata* but the dorsal margins slope more steeply, especially anteriorly, the posterior extremity is usually narrower, the shell is thicker and the hinge is heavier.

*Macoma falconensis* H. K. Hodson[68], described from the Miocene of Venezuela, is a similar species.

*Distribution*: This species was taken off Guatemala and El Salvador in 13 to 16 fathoms, usually on a muddy bottom. It also has

[68] *Macoma (Psammacoma) falconensis* H. K. Hodson, *Bull. Amer. Paleo.*, Vol. 16, No. 59, October 1, 1931, p. 16, pl. 6, figs. 1, 6, 7. "Holotype Locality—. 5 kilometers north and 350 meters west of Urumaco, in Río Codore, District of Democracia, Falcón." Venezuela. Miocene. Also other localities.

been recorded as occurring in the Pliocene of Ecuador.

**Macoma (Psammacoma) panamensis** Dall.

*Macoma (Psammacoma) extenuata* var.? *panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 310. "Panama."

*Macoma (Psammacoma) panamensis* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 324, pl. 4, fig. 3. . . . "dredged in 33 fathoms, sand, in Panama Bay."

*Type Locality*: Panama Bay, in 33 fathoms, sand.

*Range*: Gulf of California to Panama.

*Collecting Stations*: Mexico: Tenacatita Bay (183-D-3), 40 fathoms, sandy mud; 4 miles SSW. of Maldanado Point (192-D-3), 38 fathoms, mud; Tangola-Tangola Bay (196-D-18), 30 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; 14 miles S. × E. of Judas Point (214-D-1, 4,), 42-61 fathoms, mud, shell, rocks; Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sandy mud.

*Description*: Shell very elongated, slender, thin, moderately convex, right valve slightly flattened posterior to the center, inequilateral, the anterior end the longer, posterior end produced and subrostrate, yellowish-white; ornamented with fine concentric striae which are heavier on the posterior area; hinge with two teeth in each valve, the right posterior and left anterior ones cleft; pallial sinus rounded at the anterior end which projects forward about five-eights the length of the shell, and for about one-half its length confluent with the pallial line; interior of valves sometimes show obscure striations near the margins.

A right valve from the Gulf of Chiriqui, Panama, measures: length, 31 mm.; height, 14.4 mm.; convexity (one valve), 3.5 mm.; pallial sinus extends forward 20 mm. from the posterior end of the valve.

*Macoma extenuata* Dall,[69] described from the Gulf of Mexico, is a very similar species. *Macoma panamensis canalis* Olsson, described from the Miocene of the Canal Zone, is higher in proportion to the length.

Compared to *Macoma elongata* Hanley, the shell of *M. panamensis* is generally narrower and more elongate and the posterior end is narrower.

*Distribution*: This species was dredged by the expedition from off Mexico to the Gulf of Chiriqui, Panama, in 12-61 fathoms, mostly on a muddy or sandy mud bottom.

**Macoma (Psammacoma) panamensis spectri**
Hertlein & Strong subsp. nov.

Plate I, Figs. 9, 10, 16.

Shell elongate, fairly thick, white, somewhat flexed posteriorly; left valve moderately inflated, the right flattened a little posterior to the middle; posterior dorsal margin sloping, anterior end the longer, the dorsal margin slightly convex and gently sloping, that of the right overlapping the left for about a third of its length; anterior end well rounded, ventral margin only slightly curved, posterior end produced, roundly truncated, on each valve a distinct angulation extending from near the beaks to the lower end of the truncation; exterior surface showing distinct resting stages between which there are many very fine concentric striations and microscopic radial striae most distinct just anterior to the posterior angulation; fresh specimens are often iridescent; interior shining white; two cardinal teeth in each valve, the right posterior and left anterior ones bifid, lateral teeth lacking; pallial sinus subangulate above, highest at a point nearly vertically below the beaks, end elliptically rounded and extending forward about two-thirds the length of the shell and along the base for more than half its length confluent with the pallial line. Holotype, a left valve, measures: length, 34.4 mm.; height, 18.5 mm.; convexity, 5.3 mm.; pallial sinus extends anteriorly 21.5 mm. from the posterior end of the shell.

Holotype, left valve, and paratype, a right valve (Calif. Acad. Sci. Paleo. Type Coll.), dredged in Santa Inez Bay, Gulf of California, Station 143-D-3, Lat. 26° 57′ N., Long. 111° 56′ W., in 35 fathoms (64 meters), mud, crushed shell.

Three additional specimens were dredged at the same locality. Other specimens were dredged in the same general area in Santa Inez Bay at Station 143-D-1, 4, in 25-29 fathoms, mud, crushed shell, weed, sand; specimens were dredged on Arena Bank, Gulf of California, at Station 136-D-2, 45 fathoms, mud, *Arca* conglomerates. About a dozen single valves, probably from the Gulf of California, are without information as to locality. One valve from the Gulf of Chiriqui, Panama, Station 221-D-1-5, 35-40 fathoms, sandy mud, appears to belong to this subspecies.

The growth lines of these specimens are so fine that when fresh specimens are examined at an angle they act as a grating and produce beautiful iridescent spectral colors.

The shell here described as a new subspecies is similar to that of *Macoma panamensis*, but it is higher in proportion to the length and so far as known it is generally restricted to a more northern range. Some young specimens are very similar to Dall's species and perhaps additional specimens may show the form here described as new to be without significance, but the greater height, iridescent color and generally more northern distribution appear, at the present time, to be sufficient reasons for separating it as a distinct subspecies.

This new subspecies is very similar to

[69] *Macoma (Psammacoma) extenuata* Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, November, 1900, p. 314, pl. 2, fig. 7. Dredged "between the delta of the Mississippi and Cedar Keys, Florida, in 32 fathoms, sand." Cited on p. 300 as "*Macoma (Cydippina) extenuata*."

*Macoma panamensis canalis* Olsson,[70] described from the Miocene Gatun beds of Panama, which also is higher in proportion to the length as compared to *M. panamensis*. The shell of the present subspecies is higher and a little less elongate than Olsson's subspecies. Furthermore adult shells are moderately thick whereas those of Olsson's subspecies were described as very thin and fragile.

Subgenus **Psammotreta** Dall.

KEY TO THE SPECIES OF *Psammotreta*.

A. Umbos orange-red; shell subrectangular, narrow ..... *aurora*
B. Umbos white shading to ochraceous; shell proportionately larger and higher ..... *pacis*

**Macoma (Psammotreta) aurora** Hanley.

*Tellina aurora* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 147. "Hab. Panama; soft sandy mud, ten fathoms: Cuming." —Hanley, Thes. Conch., Vol. 1, 1846, p. 301, pl. 58, fig. 76. Panama.

*Macoma (Psammacoma) aurora* Hanley, Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 91, pl. 11, fig. 4. Figure of lectotype.

*Type Locality*: Panama, in 10 fathoms, soft sandy mud.

*Range*: Gulf of California to Boca de Pan, Peru.

*Collecting Stations*: Mexico: Santa Cruz Bay (195-D-21), 18 fathoms, mud; Tangola-Tangola Bay (196-D-14, 15), 5 fathoms, crushed shell; Nicaragua: Corinto (200-D-8, 9), 6-6.6 fathoms, mangrove leaves.

*Description*: Shell elongate, longer anteriorly, the end rounded, posterior end bluntly truncated, posterior area set off by an umbonal angulation; resilium internal and partly separated from the ligament; shell white or yellowish-white with the umbonal area both exteriorly and interiorly ornamented with orange red which grades into yellow anteriorly; two cardinals in each valve, the right posterior and left anterior ones faintly cleft; on some large right valves there is a small denticle-like projection of the nymph at the ventral end of the resilium; the pallial sinus extends forward about two-thirds the length of the shell to the anterior edge of the orange red area but is separated from the anterior adductor impression by considerable space; along the base for about half its length it is confluent with the pallial line.

A left valve of this species from Tangola-Tangola Bay, Mexico, in the present collection, measures 28 mm. in length. A specimen from Panama in the collections of the California Academy of Sciences, measures: length, 27.5 mm.; height, 17.3 mm.; convexity (both valves together), 8.2 mm.; pallial sinus extends forward 19 mm. from the posterior end of the shell.

The elongate, subrectangular form and orange red radial area on the umbonal region are characteristic features of this *Macoma*.

*Macoma hesperus* Dall,[71] an unfigured species described from the Gulf of Panama, was said to bear a resemblance to *M. aurora* but with a narrower shell and a different hinge.

*Distribution*: A few specimens of this species were dredged in 5-18 fathoms off west Mexico and Corinto, Nicaragua.

**Macoma (Psammotreta) pacis** Pilsbry & Lowe.

*Macoma pacis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 95, pl. 10. figs. 1, 1a, 2, 3. "La Paz, Lower California."

*Type Locality*: La Paz, Lower California.

*Range*: Gulf of California to Golfito, Gulf of Dulce, Costa Rica.

*Collecting Stations*: Mexico: Port Guatulco; Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; Costa Rica: Cedro Island, Gulf of Nicoya; Golfito.

*Description*: Shell resembling that of *Macoma aurora* but larger and higher in proportion to the length, usually whiter and tinted with yellow and on some specimens the umbonal area is of an ochraceous salmon color. Two cardinal teeth in each valve, the right posterior and left anterior ones bifid, the left posterior cardinal narrow and near the posterior margin; pallial sinus high beneath the beaks then descending to a bluntly rounded end and for about half its length confluent with the pallial line.

A specimen in the present collection from Golfito, Costa Rica, measures: length, 34.6 mm.; height, 21.8 mm.; convexity (both valves together), 9.9 mm. A large right valve from Cedro Island in the Gulf of Nicoya, measures: length, 52.6 mm.; height, 34 mm.; convexity (one valve), 6.6 mm.; pallial sinus extends forward 35 mm. from the posterior end of the shell.

Small specimens of this species are very similar to those of *Macoma aurora* but seem to differ constantly in the particular mentioned above. As pointed out by Pilsbry & Lowe the relation of height to length varies considerably in different specimens.

Illustrations of *Macoma plebeia* Hanley[72] indicate a shell which is more roundly oval with a more rounded ventral margin posteriorly. According to the illustration of that species given by Pilsbry & Lowe the pallial sinus is more broadly rounded at the end and is confluent with the pallial line for a shorter distance than that of *Macoma pacis*.

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[70] *Macoma panamensis* Dall var. *canalis* Olsson, *Bull. Amer. Paleo.*, Vol. 9, No. 39, Pt. 2, June 21, 1922, p. 429 (257), pl. 29 (26), fig. 11. "Gatun Stage; Mt. Hope, C. Z."

[71] *Macoma (Psammacoma) hesperus* Dall, *Bull. Mus. Comp. Zool.*, Vol. 43, No. 6, October, 1908, p. 421. Dredged in the "Gulf of Panama, in 182 fathoms, mud, bottom temperature 54°.1 F."

[72] *Tellina plebeia* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 147. "Hab. Real Llejos, Central America; sandy mud, seven fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 299, pl. 60, fig. 151. Original locality cited. [Not pl. 59, fig. 129. "Senegal"].

*Macoma plebeia* Hanley, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, p. 95 (in text), pl. 10, fig. 5. "Real Llejos (=Corinto)."

*Macoma mazatlanica* Deshayes[73] is very similar to *M. pacis* but is more tapering posteriorly.

*Distribution*: Specimens of *Macoma pacis* were taken by the expedition off west Mexico, Guatemala and Costa Rica. This is an extension south of the known range of the species.

Subgenus **Macoploma** Pilsbry & Olsson.

**Macoma (Macoploma) medioamericana** Olsson.

*Macoma* (*Macoploma*) *medioamericana* Olsson, *Bull. Amer. Paleo.*, Vol. 27, No. 106, December 25, 1942, p. 196 (44), pl. 17 (4), fig. 8. "Pliocene. Quebrada Peñitas, Costa Rica."

*Type Locality*: Quebrada Peñitas, Costa Rica. Pliocene.

*Range*: Arena Bank, Gulf of California, to Panama.

*Collecting Stations*: Arena Bank, Gulf of California (136-D-21), 45 fathoms, mud; El Salvador: La Libertad (198-D-2), 16 fathoms, mud; Costa Rica: off Ballena Bay, Gulf of Nicoya (213-D-11-17), 35-40 fathoms, mud.

*Description*: Shell elongate, moderately thin, general characters much like those of *Macoma elongata* but with the anterior dorsal margin more steeply sloping and with the posterior area ornamented with strong concentric laminae and earthy granules.

The largest specimen in the collection from the Gulf of Nicoya, measures approximately: length, 101 mm.; height, 54 mm.; convexity (both valves together), 24 mm.

Some of the specimens in this collection agree so closely with Olsson's description and illustration of *Macoma medioamericana* that we have referred them to his species. There is variation in the specimens and some might be equally well referred to *Macoma* (*Macoploma*) *ecuadoriana* Pilsbry & Olsson[74] described from the Pliocene of Ecuador. According to Olsson, *M. medioamericana* is proportionately longer and has coarser and more earthy granulations on the posterior submargins in comparison to *M. ecuadoriana*.

It is obvious from a study of a series of specimens that there are several very closely related variable species, including *Macoma elongata*, *M. panamensis*, *M. lamproleuca*, *M. ecuadoriana* and *M. medioamericana*. The presence of granulation on the posterior areas appears to be the only certain criterion separating the species of *Macoploma* from some of the others. The granules are present on specimens in the present collection after they have attained a length of about 20 to 25 mm. It is very difficult to separate specimens of a smaller size from those of *M. elongata* or *M. lamproleuca*.

[73] *Tellina mazatlanica* Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 359. "Hab. Mazatlan. Coll. Cuming." —Sowerby, Conch. Icon., Vol. 17, *Tellina*, October, 1868, species 320, pl. 54, fig. 320. "Hab. Mazatlan. Coll. Cuming."

[74] *Macoma* (*Macoploma*) *ecuadoriana* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 69, pl. 19, fig. 5. "Canoa formation, Punta Blanca." Ecuador, Pliocene.

*Distribution*: Specimens of this species were dredged by the expedition at depths of 16 to 45 fathoms from Arena Bank, Gulf of California, La Libertad, El Salvador, and off Costa Rica in the Gulf of Nicoya, mostly on a muddy bottom. The species also is known to occur in the Pliocene of Costa Rica. The present records of occurrence reveal for the first time that this species is living at the present time in west American waters.

Genus **Apolymetis** Salisbury.

KEY TO THE SPECIES OF *Apolymetis*.

A. Posterior end broadly rounded
  a. Shell thick, hinge broad ... *biangulata*[75]
  aa. Shell thin, hinge narrow ..... *cognata*
B. Posterior end tapering, truncated
  a. Hinge fairly broad; anterior adductor impression elongately oval; pallial sinus for a little less than half its length confluent with pallial line ..... *dombei*
  aa. Hinge very narrow; anterior adductor impression very long and narrow; pallial sinus confluent with pallial line for only a very short distance *asthenodon*[75]

**Apolymetis cognata** Pilsbry & Vanatta.

*Lutricola cognata* Pilsbry & Vanatta, *Proc. Washington Acad. Sci.*, Vol. 4, September 30, 1902, p. 556, pl. 35, fig. 5. "From Tagus Cove, Albemarle." Galápagos Islands.

*Apolymetis cognata* Pilsbry & Vanatta, Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, 1932, pp. 96 (in text), 133. Galápagos Islands, also Taboga Island, Panama, and Corinto, Nicaragua.

*Type Locality*: Tagus Cove, Albemarle Island, Galápagos Islands.

*Range*: Magdalena Bay, Lower California, to Paita, Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: Shell rounded-quadrate, moderately compressed, bent to the right posteriorly, rather thin, gray white. Sculptured with irregular growth wrinkles and low radial striae, covered with an extremely minute secondary radial striation. Beaks median, worn at the tip. Anterior margin rounded; posterior margin subtruncate, the basal margin straightened, sinuous; pallial sinus ample. Length of left valve, 41 mm., alt. 34 mm., diameter 8 mm. (Original description).

Closely related to *L. alta* Conr., but higher, shorter, of a more quadrate shape. The anterior end of the pallial sinus is more rounded, and its upper margin is not sinuous. *L. excavata* Sowb. is a more wedge-shaped shell (Pilsbry & Vanatta).

This species differs from the generally more northern *A. biangulata* Carpenter in the much narrower, weaker hinge, in the more flaring and less steeply sloping posterior area, and in the generally thinner shell.

[75] Not represented in the present collection.

Specimens referable to the present species from the Gulf of California and southward have in some instances, formerly been referred to "*Tellina*" *excavata* Sowerby[76] which was originally described without information as to locality. As pointed out by Pilsbry & Vanatta the illustration given by Sowerby indicates a shell with the posterior end wedge-shaped. Pilsbry & Lowe later pointed out that there seemed to be no characters by which "*Tellina*" *excavata* could be separated from *Apolymetis dombei* Hanley. They recognized only four west American species of the genus, *Apolymetis alta* Conrad [=*biangulata* Carpenter], *A. asthenodon* Pilsbry & Lowe, *A. cognata* Pilsbry & Vanatta and *A. dombei* Hanley. However for some unexplained reason, probably an oversight, they cited (p. 195) *A. excavata* Sowerby from Mazatlan, Mexico. In later publications, Lowe[77] cited "*Metis excavata* Sowerby" as occurring at Punta Penasco, Mexico, in the Gulf of California, and Pilsbry & Olsson[78] recorded "*Apolymetis excavatus* Sowerby" from the Pliocene of Ecuador. No illustrations were given of the shells representing those records so we are uncertain which species was represented. Specimens from the coast of the mainland appear to be identical with those from the Galápagos Islands, the type locality of *A. cognata*.

*Distribution*: A single small right valve of this species, measuring about 20 mm. in length, was taken by the expedition at Corinto, Nicaragua, in 12-13 fathoms.

**Apolymetis dombei** Hanley.

*Tellina dombei* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 144. "Hab. Panama; twelve fathoms, sandy mud."—Hanley, Thes. Conch., Vol. 1, 1846, p. 323, pl. 62, fig. 182. Panama. Variety, pl. 64, fig. 222. Tumbez, Peru.

*Tellina dombeyi* Hanley, *Proc. Zool. Soc. London* for 1844 (issued February, 1845), p. 195 (index).—Sowerby, Conch. Icon., Vol. 17, *Tellina*, 1867, species 169, pl. 30, fig. 169. "Hab. Panama, Tumbez, Peru."—Römer, Syst. Conchyl.-Cab. von Martini und Chemnitz, Bd. 10, Abt. 4, *Tellina*, 1871, p. 205, pl. 39, figs. 7-9. Various localities cited from the Gulf of California to Tumbez, Peru.

*Psammobia* sp., Li, *Bull. Geol. Soc. China*, Vol. 9, No. 3, 1930, p. 262, pl. 5, fig. 32. Dredged in Panama Bay in 10-40 ft. "Probably Gatun formation." Pilsbry (*Proc. Acad. Nat. Sci. Philadelphia*, Vol. 83, 1931, p. 431) stated that Li's record was based on "A good but bleached valve of *Apolymetis dombei* (Hanley)."

*Type Locality*: Panama, in 12 fathoms, sandy mud.

*Range*: Gulf of Fonseca to Tumbez, Peru.

*Collecting Stations*: Nicaragua: Potosi and 5 miles SSW. of Monypenny Point, Gulf of Fonseca, beach; Costa Rica: 1 mile S. of entrance to Golfito Bay, Gulf of Dulce, beach.

*Description*: Shell ovately subtrigonal, moderately thick, rather smooth, white but often with umbonal area reddish-orange exteriorly and sometimes interiorly; the anterior end the longer, rounded and somewhat obliquely produced; a flexure or depressed radial area is present anterior to the posterior umbonal ridge; posterior end sloping, subtriangular and subtruncated, area set off by an umbonal angulation; hinge with two cardinals, the right posterior bifid, the left anterior grooved, no laterals present; the pallial sinus is high and subangulate in the middle then sloping down even with but well separated from the anterior adductor impression and for a little less than one-half its length confluent with the pallial line.

The shell of this species is somewhat variable in outline. Some specimens agree almost exactly with Hanley's original figure, others are more trigonal. A large right valve from the Bay of Panama in the collections of the California Academy of Sciences, measures: length, 66 mm.; height, 51 mm.; convexity (one valve), 14 mm.

Römer, 1871, and Stearns, 1891, pointed out the resemblance between "*Tellina*" *dombei* and "*Tellina*" *excavata* Sowerby[79] which was described without information as to the locality from which it came. Later Pilsbry & Lowe, 1932, stated that they knew of no difference separating these two species.

Compared to *Apolymetis dombei*, *A. asthenodon* Pilsbry & &Lowe[80] was described as possessing a more elongate shell with a very narrow hinge, a narrower, longer anterior adductor impression. Judging from the illustrations, the pallial sinus is confluent with the pallial line for a very short distance if at all.

The shell of *Apolymetis dombei* differs from that of *Macoma grandis* Hanley[81] which was originally described from Tumbez, Peru, and was taken at Corinto, Nicaragua, by the Templeton Crocker Expedition, 1932, in the stronger, broader, posterior umbonal fold and much longer pallial sinus. Judging from the illustration of *Macoma gubernaculum* Hanley,[82] originally described from Real

[76] *Tellina excavata* Sowerby, Conch. Icon., Vol. 17, *Tellina*, March, 1867, species 138, pl. 26, fig. 138. "Hab.—?"

[77] Lowe, H. N., *Trans. San Diego Soc. Nat. Hist.*, Vol. 8, No. 6, 1935, p. 28.

[78] Pilsbry, H. A., and Olsson, A. A., *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, 1941, p. 70.

[79] *Tellina excavata* Sowerby, Conch. Icon., Vol. 17, *Tellina*, March, 1867, species 138, pl. 26, fig. 138. "Hab.—?"

Soot-Ryen (*Nyt. Mag. for Naturvid.*, Bd. 70 (Meddel. Zool. Mus. Oslo, No. 27), 1932, p. 321, pl. 2, fig. 10) illustrated a shell under the name of *Apolymetis excavata* Sowerby from Floreana (Charles) Island, Galápagos group. He remarked on the variability of the outer form revealed by different specimens, some of which were elongated, other shorter and higher.

[80] *Apolymetis asthenodon* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 96, pl. 11, figs. 1-3. "Panama, on the beach (D. E. Harrower, J. Zetek)." Type. Also at La Union, Gulf of Fonseca, El Salvador.

[81] *Tellina grandis* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 141. "Hab. Tumbez, Peru." —Hanley, Thes. Conch., Vol. 1, 1846, p. 327, pl. 65, fig. 247. Tumbez, Peru.

[82] *Tellina gubernaculum* Hanley, *Proc. Zool. Soc. London*, December, 1844, p. 142. "Hab. Real Llejos, Central America; in sandy mud, seven fathoms." —Hanley, Thes. Conch., Vol. 1, 1846, p. 325, pl. 62, fig. 186. "Real Lejos, Central America (Cuming)."

Llejos, Nicaragua, the anterior dorsal margins slope more abruptly than those of *A. dombei*.

*Distribution*: Specimens of *Apolymetis dombei* were taken by the expedition on the beaches in the Gulf of Fonseca, Nicaragua, and Gulf of Dulce, Costa Rica. We have not seen specimens from north of Nicaragua. It has been reported as ranging south to Peru. It also has been recorded as occurring in beds of upper Pliocene age in the Galápagos Islands. "*Apolymetis* cf. *A. dombei* (Hanley)" has been cited by Stewart[83] as occurring in upper Pliocene beds in the Kettleman Hills, San Joaquin Valley, California.

### Genus **Strigilla** Turton.

KEY TO THE SPECIES OF *Strigilla*.

A. Shell equilateral; small, white ..... *lenticula*
B. Shell inequilateral, elongated posteriorly
  a. Striae much more widely spaced anteriorly ..... *cicercula*
  aa. Striae equally or more closely spaced anteriorly
    b. Shell thick; convex; roundly truncated anteriorly ..... *costulifera*
    bb. Shell thin; flatter; expanded anteriorly ..... *disjuncta*

#### **Strigilla cicercula** Philippi.

Plate I, Fig. 19.

*Tellina cicercula* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 19. "Patria: Mazatlan."

*Tellina dichotoma* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 20. "Patria: Mazatlan."

*Tellina ervilia* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 20. "Patria: Mazatlan."

*Strigilla maga* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. "Sonsonate." El Salvador.

*Strigilla interrupta* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 190. "Sonsonate." El Salvador.

*Strigilla circercula* Philippi, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 305. Gulf of California to Panama.

*Type Locality*: Mazatlan, Mexico.

*Range*: Gulf of California to Ecuador.

*Collecting Station*: Nicaragua: Corinto (200-D-11, 19, also beach), 8-13 fathoms, sand, mangrove leaves.

*Description*: Shell small, usually less than 1 cm. in length, rounded, elongated posteriorly, polished, white, with pink color usually confined to the umbonal region; sculptured with fine radial striae which on the anterior area are curved and very much more widely spaced.

A large right valve of this beautiful little species, dredged off Corinto, Nicaragua, in 13 fathoms, measures: length, 9.5 mm.; height, 8.5 mm.; convexity (one valve), 2.5 mm.

The smaller size, pink colored umbonal area, and much wider spaced sculpture on the anterior area, are characters which serve to separate the shell of *Strigilla cicercula* from that of the young of *S. costulifera* Mörch.

*Strigilla pisiformis* Linnaeus, which occurs in the Caribbean region, is a very similar species.

*Distribution*: This species was collected by the expedition at Corinto, Nicaragua, on the beach and dredged at depths of 8 to 13 fathoms.

#### **Strigilla costulifera** Mörch.

Plate I, Fig. 15.

*Tellina carnaria* Linnaeus, Hanley, Thes. Conch., Vol. 1, 1846, p. 260 (in part), pl. 56, fig. 38 [West Colombia record only].

Not *Tellina carnaria* Linnaeus. Caribbean region.

*Tellina* (*Strigilla*) *fucata* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 91. Pacific coast [No exact locality cited].—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, October, 1853, p. 399, pl. 16, fig. 4. "Inhabits Mazatlan."

Not *Tellina fucata* Hinds, Zool. Voy. Sulphur, Moll., Pt. 3, 1844, p. 67, pl. 21, fig. 4.

*Strigilla costulifera* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. "Sonsonate." El Salvador.

*Tellina chroma* Salisbury, *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 84. New name for *Tellina* (*Strigilla*) *fucata* Gould, 1851, not *Tellina fucata* Hinds, 1844.

*Type Locality*: Sonsonate, El Salvador.

*Range*: Magdalena Bay, Lower California, to the Gulf of California and south to Ecuador.

*Collecting Stations*: Mexico: Tenacatita Bay, beach; Sihuatanejo Bay, beach; Nicaragua: Corinto (200-D-16), 4-7 fathoms, mangrove leaves.

*Description*: Shell suborbicular, the anterior side much the shorter, moderately thick, glossy, pink, rose or white ringed with pink or carmine; umbos smooth; the ornamentation consists of striae, anteriorly flexuous, forming an angle with those on the central area, which usually radiate obliquely posteriorly; on the posterior slope the striae are fine and usually meet at an acute angle; a lunule present; hinge with a bifid cardinal and two laterals in each valve; one or two thickened rays often present interiorly; the pallial sinus touches the anterior adductor impression and is confluent with the pallial line below; the interior is often of a beautiful deep red or carmine color.

Dall pointed out that the shell of this species is very inconstant in details of sculpture, color, and in the presence or absence of a smooth radial streak on each valve.

A very large specimen of this species from Magdalena Bay, Lower California, in the

[83] *Apolymetis* cf. *A. dombei* (Hanley), Stewart, *U. S. Geol. Surv., Prof. Paper 195*, 1940 (issued June 7, 1941), p. 93, pl. 32, fig. 2. *Siphonalia* zone in North Dome, Kettleman Hills, San Joaquin Valley, California. Etchegoin formation, upper Pliocene.

Henry Hemphill collection of the California Academy of Sciences, measures approximately: length, 25 mm.; height, 23 mm.; convexity (both valves together), 10.3 mm. The specimens in the present collection are smaller.

*Strigilla costulifera* is very similar to the east American *S. carnaria* Linnaeus. The west American shell is often somewhat more rounded and the striae appear to be less numerous.

*Distribution*: Specimens of *Strigilla costulifera* were taken by the expedition on the beaches along western Mexico and dredged in 4 to 7 fathoms at Corinto, Nicaragua.

**Strigilla disjuncta** Carpenter.

Plate I, Fig. 20.

*Strigilla disjuncta* Carpenter, *Proc. Zool. Soc. London*, November 11, 1856, p. 160. "Hab. In Sinu Panamensi; legit. T. Bridges."

*Type Locality*: Bay of Panama.

*Range*: Corinto, Nicaragua, to Panama.

*Collecting Station*: Nicaragua: Corinto (200-D-11), 8 fathoms, sand.

*Description*: S. testa satis magna, alba, tenui, planata; inaequilaterali, postice producta; marginibus dorsalibus subrectis, ad angulam 120°, aliis bene arcuatis; lineis incrementi vix monstrantibus; lineis undulatis exillimis, antice concentricis, umbones versus ascendentibus, sinu angustiore; dein ad marginem ventralem rapide descendentibus; dein subito, angulo acuto, circiter 20° postice rursus ascendentibus; lineis angularum in valva utraque haud convenientibus; margine postico sinuato, sculptura postea fortiore; margine antico quoque sinuato; lunula distincta, sinuata; ligamento subelongato; dent card. valva altera uno parvo et uno magno bifido; altera uno parvo bifido; dent. lat. acutioribus, haud distantibus. Long. 1.35, lat. 1.54, alt. .54 poll. (Original description).

"Allied to *S. sincera* Hanl.; remarkable for its large size and very fine markings, and named from the lines of markings in the two valves not agreeing at the edges." (Carpenter).

Compared to *Strigilla costulifera* Mörch, the shell of *S. disjuncta* is usually larger and the shell is thinner, flatter, more produced anteriorly, the beaks are more projecting and beneath them the dorsal margin is more concave. It is generally white or white tinged with pink.

A large specimen collected at Panama by James Zetek measures: length, 36 mm.; height, 31 mm.; convexity (both valves together), 13.8 mm.

This species has been cited from west American waters under the name of *Strigilla sincera* Hanley[84] which, according to Hedley[85], is an Australian species. Salisbury[86] in 1934 stated that *Strigilla sincera* occurs in the Panamic area but he did not mention Hedley's remarks on that species.

*Distribution*: Two single valves of this species were dredged by the expedition at Corinto, Nicaragua, in 8 fathoms, and one valve was taken on shore. This is an extension north of the known range of the species.

**Strigilla lenticula** Philippi.

Plate I, Fig. 21.

*Tellina lenticula* Philippi, *Zeit. f. Malakozool.*, Jahrg. 3, February, 1846, p. 19. "Patria: Mazatlan."

*Strigilla serrata* Mörch, *Malakozool. Blätter*, Bd. 7, December, 1860, p. 189. Central America.

*Strigilla lenticula* Philippi, Dall, *Proc. U. S. Nat. Mus.*, Vol. 23, No. 1210, 1900, p. 305. Cape San Lucas to Central America.

*Type Locality*: Mazatlan, Mexico.

*Range*: Cape San Lucas, Lower California, to Corinto, Nicaragua.

*Collecting Stations*: Nicaragua: Corinto (200-D-11, 17, 19, also on beach), 7-13 fathoms, sand, mangrove leaves.

*Description*: Shell small, about 8 mm. in length, rounded, inflated, white, sculptured with well-developed, oblique, incised striae which posteriorly develop small chevron-shaped sinuations.

A large right valve of this species, dredged off Corinto, Nicaragua, in 13 fathoms, measures approximately: length 8 mm.; height, 7 mm.; convexity (one valve), 2.7 mm.

The rounded form, white color, and slight development of V-shaped sinuations in the sculpture posteriorly are characters which easily serve to separate this species from others of the genus in west American waters.

*Strigilla flexuosa* Say, an east American species, is a very similar form.

*Distribution*: This little species was taken by the expedition only at Corinto, Nicaragua, on the beach and at depths of 7-13 fathoms.

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[84] *Tellina sincera* Hanley, *Proc. Zool. Soc. London*, April, 1844, p. 68. "Hab.—? Mus. Cuming, Metcalfe." —Hanley, Thes. Conch., Vol. 1, 1846, p. 261, pl. 60, fig. 144. [Not the record "N. W. Coast of America, (Dr. Sinclair)," according to Hedley].

[85] *Strigilla sincera* Hanley, Hedley, *Proc. Linn. Soc. New South Wales*, Vol. 38, Pt. 2, 1913, p. 272. *Strigilla grossiana* Hedley, 1908, was considered by Hedley to be a synonym of *S. sincera* Hanley.

[86] Salisbury, A. E., *Proc. Malacol. Soc. London*, Vol. 21, Pt. 2, July, 1934, p. 89.

## EXPLANATION OF THE PLATE.

### Plate I.

Fig. 1. *Tellina* (*Moerella*) *felix* Hanley. Hypotype, right valve, from Monypenny Point, Gulf of Fonseca, Nicaragua. Length, 17 mm.; height, 10 mm. View of exterior. P. 70.

Fig. 2. *Tellina* (*Moerella*) *recurvata* Hertlein & Strong, sp. nov. Holotype, right valve, from Loc. 23802 (C.A.S.), San Luis Gonzaga Bay, Lower California, in the Gulf of California. Length, 12 mm., height, 7.5 mm. P. 71

Fig. 3. *Tellina* (*Moerella*) *recurvata* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 2.

Fig. 4. *Tellina* (*Moerella*) *recurvata* Hertlein & Strong, sp. nov. Holotype, left valve. View of the exterior of the left valve of the specimen shown in Figs. 2 and 3.

Fig. 5. *Tellina* (*Moerella*) *arenica* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-20, Lat. 23° 30′ N., Long. 109° 26′ W., Arena Bank, Gulf of California, dredged in 43 fathoms (78 meters), mud. View of interior. P. 68.

Fig. 6. *Tellina* (*Merisca*) *proclivis* Hertlein & Strong, sp. nov. Holotype, left valve, from Loc. 20299 (C.A.S.), Magdalena Bay, Lower California, Mexico. Length, 9 mm.; height, 7.8 mm. View of interior. P. 83.

Fig. 7. *Tellina* (*Merisca*) *proclivis* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 6.

Fig. 8. *Tellina* (*Moerella*) *recurvata* Hertlein & Strong, sp. nov. Paratype, right valve, from the same locality as the holotype shown in Figs. 2, 3 and 4. Length, 11.5 mm.; height, 7 mm.

Fig. 9. *Macoma* (*Psammacoma*) *panamensis spectri* Hertlein & Strong, subsp. nov. Paratype, right valve, from Station 143-D-3, Lat. 26° 57′ N., Long. 111° 56′ W., Santa Inez Bay, Lower California, in the Gulf of California, dredged in 35 fathoms (64 meters), mud, crushed shell. Length, 33.8 mm.; height, 18 mm. P. 91.

Fig. 10. *Macoma* (*Psammacoma*) *panamensis spectri* Hertlein & Strong, subsp. nov. Paratype. View of the interior of the specimen shown in Fig. 9.

Fig. 11. *Tellina* (*Moerella*) *arenica* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 5.

Fig. 12. *Tellina* (*Tellinella*) *zacae* Hertlein & Strong, sp. nov. Holotype, right valve, from Station 136-D-1, Lat. 23° 29′ N., Long. 109° 25′ W., Arena Bank, Gulf of California, dredged in 45 fathoms (82 meters), mud. Length, 33.4 mm.; height, 15.2 mm. P. 65.

Fig. 13. *Tellina* (*Tellinella*) *zacae* Hertlein & Strong, sp. nov. Holotype, left valve. View of the interior of the left valve of the specimen shown in Fig. 12.

Fig. 14. *Tellina* (*Merisca*) *proclivis* Hertlein & Strong, sp. nov. Holotype. Right valve of the specimen shown in Figs. 6 and 7.

Fig. 15. *Strigilla costulifera* Mörch. Hypotype, right valve, from Loc. 4798 (C.A.S.), Lower California; Henry Hemphill Coll. Length, 25 mm.; height, 22 mm. P. 95.

Fig. 16. *Macoma* (*Psammacoma*) *panamensis spectri* Hertlein & Strong, subsp. nov. Holotype, left valve, from the same locality as the paratype shown in Figs. 9 and 10. Length, 34.4 mm.; height, 18.4 mm. P. 91.

Fig. 17. *Tellina* (*Tellinella*) *zacae* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 13. P. 65.

Fig. 18. *Tellina* (*Eurytellina*) *inaequistriata* Donovan. Hypotype, right valve, from Station 195-D-21, Lat. 15° 44′ 45″ N., Long. 96° 06′ 55″ W., Santa Cruz Bay, Mexico, dredged in 18 fathoms (33 meters), mud, crushed shell. Length, 23 mm.; height, 12.5 mm. P. 74.

Fig. 19. *Strigilla cicercula* Philippi. Hypotype, right valve, from Station 200-D-19, Lat. 12° 28′ 03″ N., Long. 87° 12′ 39″ W., Corinto, Nicaragua, dredged in 12-13 fathoms (22-24 meters), mangrove leaves. Length, 9.6 mm.; height, 8.5 mm. P. 95.

Fig. 20. *Strigilla disjuncta* Carpenter. Hypotype, right valve, from Panama; James Zetek Coll. Length, 36 mm.; height, 31.3 mm. P. 96.

Fig. 21. *Strigilla lenticula* Philippi. Hypotype, right valve, from the same locality as the specimen shown in Fig. 19. Length, 7.9 mm.; height, 7.0 mm. P. 96.

Fig. 22. *Tellina* (*Eurytellina*) *planulata* Sowerby. Hypotype, left valve, from 1 mile south of entrance to Golfito Bay, Costa Rica. Length, 51.8 mm.; height, 29.5 mm. P. 76.

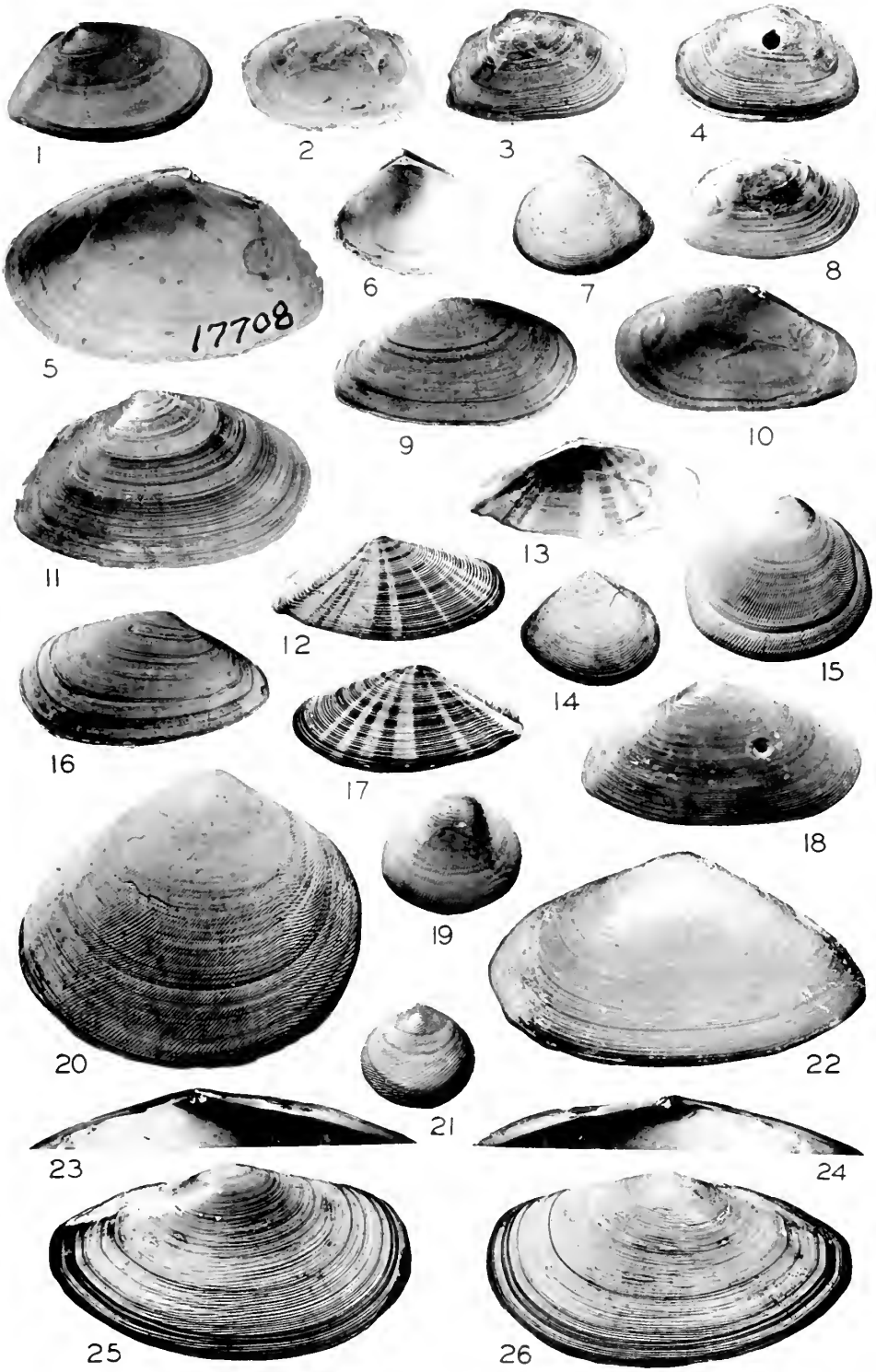
Fig. 23. *Tellina* (*Scissula*) *nicoyana* Hertlein & Strong, sp. nov. Holotype, right valve, from Ballena Bay, Costa Rica. Length, 34.4 mm.; height, 19 mm. View of hinge. P. 85.

Fig. 24. *Tellina* (*Scissula*) *nicoyana* Hertlein & Strong, sp. nov. Holotype, left valve. View of hinge.

Fig. 25. *Tellina* (*Scissula*) *nicoyana* Hertlein & Strong, sp. nov. Holotype, right valve. View of the exterior of the specimen shown in Fig. 23. P. 85.

Fig. 26. *Tellina* (*Scissula*) *nicoyana* Hertlein & Strong, sp. nov. Holotype, left valve. View of the exterior of the specimen shown in Fig. 24. P. 85.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.




MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA.

# 10.

## Fishes That Rank Themselves Like Soldiers on Parade.

E. W. GUDGER.
*American Museum of Natural History.*

(Plate I; Text-figures 1 & 2).

### INTRODUCTION.

I have read that some mammals, such as the American bison and the antelopes of South Africa, advance, wheel and deploy in something like military order. But it is doubtful if they form in ranks with heads in a real military formation. We all know that migrating birds fly in fair formation and some writers have alleged that some aquatic birds will fish in synchronous order. But so far as known, no one seems to have produced photographic evidence of this latter alleged behavior.

For reptiles we apparently have no photographic evidence, but there are at least two written accounts that surely establish the matter of ranked formation. The first of these is from the pen of the old naturalist, William Bartram. In 1774 (Travels through North and South Carolina, Georgia, and . . . Florida, etc. London, 1792, p. 118), while ascending the St. Johns River in eastern Florida, he found great numbers of huge and very aggressive alligators. Some of these threatened attacks on his little boat, when he sought to go into a lagoon off the river to catch some fish for his supper. He says—"I . . . made good my entrance into the lagoon, though not without opposition from the alligators who formed a line across the entrance but did not pursue me into it." Here the alligators were ranked in a line, apparently waiting for the fishes to try to get out into the main stream, when the alligators too would get their supper.

This account is counterbalanced by a parallel description of what C. R. S. Pitman (A Game Warden Among his Charges, London, 1931, p. 248) saw just below Murchison Falls on the Nile River in East Central Africa, where crocodiles are found in incredible numbers. "Looking from above on a still evening, one will be struck by the regular formation taken up by row after row of crocodiles, like ships of war, with intervals of about 50 feet between each crocodile [and those on either side] and 300 feet between the rows, which extend from bank to bank and for about two miles down stream." But let a fish come down and all is wild confusion and struggle of the neighboring crocodiles to get it or at least a portion of it.

The more we know about animals, the more we find them doing unusual and unexpected things. It is not safe offhandedly to contradict accounts by non-scientific observers of unusual behavior not otherwise physically impossible—in fishes, as well as in other animals. No article has been found in this search describing regimented fishes and bearing such a title as that at the head of this report. However, there is widely scattered evidence that fishes do "fall in and form ranks." Unfortunately, I have never had the opportunity to see fishes take on a military formation but various reputable observers have, and their cumulative evidence will now be set forth chronologically.

### FISHES RANKED LIKE SOLDIERS ON PARADE.

The earliest account of ranked fishes found in this search is by a writer in The New Monthly Magazine, 1820, part II, p. 137, who signs himself "Amateur." This account is also found in Thomas Boosey's "Anecdotes of Fish and Fishing," London, 1887, p. 123.

"Amateur", in writing of the exploits of one Darcey of Oxford, an expert swimmer and diver, who caught fishes with his hands in a deep hole well-known to Oxonians, makes the following statement:—

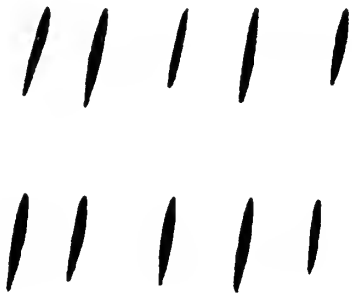
> The report that Darcey made, was that many of these fish [barbel] lay with their heads against the bank, in parallel line, like horses in their stalls. They were not disturbed at his approach, but allowed him to come close and select the finest.

In talking over this unusual matter with my long-time friend, the late Dr. John L. Peters, an upstate New York man, he told me that in his boyhood he had seen this very thing in a stream in Ulster County. At my request he prepared a statement of his observations, which is the earliest American evidence that has come to hand.

In 1907 or 1908, while trout-fishing in the headwaters of Woodland Stream in Ulster Co., New York, my attention was called to the

peculiar formation of some brook trout after a disturbed pool had quieted down. They seemed to line up in a formation as if some military officer among them had got them ready for a parade. This I saw more than once since I used to go out of my way to watch the trout in this pool. When disturbed, they would scatter, but when things quieted down, they would again take on their military formation.

This pool was just below a little rapid in a narrow stream. It was about 8 feet wide, 3 feet deep at its head and about 6 or 8 inches at its shallow end. Dr. Peters drew a little diagram (Text-fig. 1) to show how the fishes were ranked.



TEXT-FIG. 1. Diagram of trout on parade, in Woodland Stream, Ulster County, New York, 1907 or 1908. Sketch by Dr. John L. Peters.

Chronologically our next evidence is in a personal communication from Mr. Joshua W. Atlee of Riverton, New Jersey. He wrote that in October, 1911, he saw ranked fishes in a pool in a rivulet flowing into the Bay of Chaleur, Gulf of St. Lawrence. Carefully pushing aside the shrubbery on the bank of the pool, he had a clear view of it and its piscine inhabitants, which he thought were getting ready for spawning. Of these fishes he noted that:

An interesting feature of the sight was the fact that in the slowly moving water, due to the [small] volume of the pool, the fish lay in "sardine fashion" closely packed with heads upstream, stemming the current so as to retain a similar relative position by the slight movement of their tails and fins.

Finally on being disturbed, some left the pool in various directions, mostly upstream; but my guide, detouring and getting into the stream above them, actually drove many of the trout back into the pool, where they finally settled down again as we had first found them.

My next evidence is from Mr. Howard B. MacDonald of Yonkers, N. Y., a traveler and lecturer of wide experience. A photograph taken by him at Rotorua, New Zealand, in 1925, is reproduced as Plate I, Fig. 1. Of it he wrote (personal communication) as follows:

Unfortunately, the photograph does not show the fish in quite such straight lines as the other picture you have. However, these fish I saw did act in the same manner as the ones you are studying. Each fish had a certain definite position in relation to the others of this company; and if the fish were disturbed by throwing a stone into the water near them (as we all did) then they would scatter, but each would return almost immediately to his same position in the group. This was checked and verified by observation many times and there is no doubt but that each fish knew his correct position and always went to it.

Here is the word of another reliable observer, backed by photographic evidence. As Mr. MacDonald says, this is not such as may be seen in Plate I, Fig. 2, but discounting shadows, the fish are in pairs and they are lined up fairly well in ranked rows.

And now follows an excerpt from a personal communication from Dr. Louise M. Perry, long a winter resident of Sanibel Island off Fort Myers, southwest coast of Florida. Dr. Perry, an acute observer for many years of the habits of marine fishes in that region, writes as follows under date of July 26, 1926:

Naples, Florida [below Fort Myers], has a fine pier for still fishing, and while waiting for bites, I have repeatedly watched small schools of snook (rovalle) 8 or 12 in a group, lying on the sandy bottom, close together and parallel with each other, all heading the same way and all their tails gently moving to right and left in perfect unison. Suddenly with a rush they would dart into a school of minnows and play havoc for a moment, then each would gently settle down in its former place and position. This performance would be repeated at fairly regular intervals for a long time, and always made me wonder how separate individual actions could be so perfectly synchronized. How do they do it? What is the stimulus that keeps all the tails waving to marching time and starts the snook off in a simultaneous dash after the little fish?

Specific attention is called to the fact that all the tails of these marine fishes moved to right and left in perfect unison. And so did the tails of the freshwater fishes observed by Mr. Atlee in 1911 in the rivulet flowing into the Bay of Chaleur, Gulf of St. Lawrence. Presumably the same purpose activated both lots of fishes—to maintain position.

And now, also in 1926, come three accounts of this behavior of other marine fishes at the Galápagos Islands, from the pen of that veteran observer, William Beebe, in his "Arcturus Adventure" (New York, 1926). On p. 54 he states that they paid out strings with pieces of bait and enticed three sharks alongside their boat. Here follows his description of the behavior of a large shark and its attendants.

. . . by pulling in the tempting morsel two feet in front of the eager blunt snouts, we brought them to the surface directly under our feet, so that we could watch the movements of the brilliant blue pilotfish, that . . . anticipated every movement of their huge patrons. One of the big fellows had three of these little satellites that unfailingly held their formation, one just above his head, the other two in perfect alignment a few inches in front of his jaws. So exactly synchronized are the movements . . . that

it is impossible to tell whether the shark follows the pilotfish or the pilotfish the shark.

Again Beebe (1926, p. 183) notes that:

> Two mighty schools of *Xesurus laticlavius* [the yellow-tailed surgeonfish] passed me grazing slowly. When within six feet, they left off their eternal feeding and formed up into more or less orderly ranks which flowed like some enormously long sea-serpent around the identical corners of rocks where had passed the leaders, yards and yards in advance. Invariably the formation of an irregular line led very close to me, the closing up of ranks evidently being connected with the presence of danger or at least something suspicious or strange.

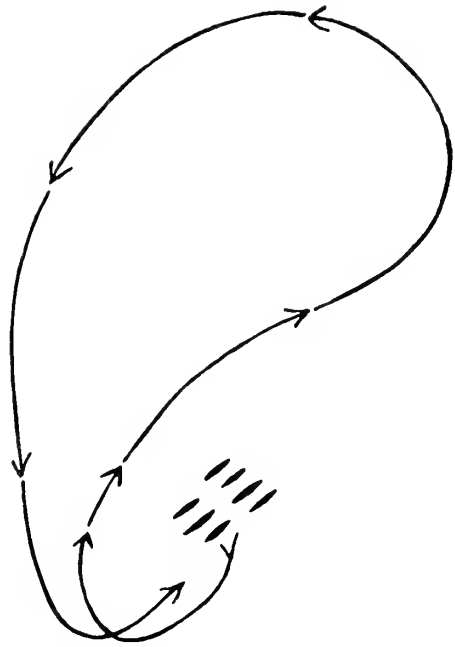
Further, Beebe (1926, pp. 290-291) makes note of another synchronous action of the yellow-tailed surgeonfish: "Several hundred approached swimming slowly along, when, as if at a signal, all would stop, and over a rather flat bottom would up-end like ducks and begin to graze ["on the plant and animal fodder which covers the rocks," p. 290].

On February 27, 1929, the late Prof. M. M. Metcalf wrote—"I am sending you some quotations [copied] from an old letter. These . . . aroused my interest at the time the observations were made some years ago." These observations were by another man, and lacking a name and date, will be entered under date (1929) of the covering letter. The pertinent quotation reads as follows:

> . . . I saw in the clear pool below Trick Falls in the Two Medicine River in Glacier National Park seven trout behaving in a way that seemed interesting. They were headed into the current and were lying motionless in two perfectly straight rows, four in the front row and three in the back row, aligned as accurately as a squad of well drilled soldiers. A moth came flipping over the pool, touching the water now and then. All the trout remained quiet, except that the right trout in the rear row turned to the right and backed around the left end of the squad, caught the moth, returned around the left end of the squad to his place at the right end of the rear row again, and they all remained in perfect formation for the several minutes I watched them.

On the margin of the typed sheet is a pencil sketch of the movements of the trout at the right hand end of the second rank. This is reproduced herein as Text-fig. 2, and is a graphic presentation of the interesting action of this particular fish.

The well-known sports magazine, Field and Stream, for November, 1929, p. 104, has reproduced the splendid photograph shown in Plate I, Fig. 2. It is also reproduced (in larger size) in the same journal for June, 1935, p. 44. But in neither issue is there any account of the phenomenon, marvellous as it is. The 1929 figure has this caption: "A most extraordinary photograph of resting trout in the Brule River, 40 miles from Duluth, Minnesota. Note the very unusual formation—like soldiers on parade." The 1935 issue has a caption which remarks that "When great schools of fish lie in still water, it takes a skillful angler to interest them" — and nothing about military formation in the article in which the figure is set.



TEXT-FIG. 2. Trout in two ranks in Two Medicine River, Glacier National Park. The right trout in row two, backed out and followed the course indicated to catch a moth dipping in the water, and then returned to his position. Sketch furnished by Prof. M. M. Metcalf, 1929.

Here is a priceless photograph showing eight rows of "trout on parade." It is apparently the only one ever published of this unique, indeed phenomenal, behavior of fishes, and there is no word of comment beyond the caption. It seems incredible, but such is the fact. However, the figure splendidly illustrates the accounts quoted above. But before going further, the present writer submits the following remarks.

Trout at rest in running water always face upstream. In pools, especially small ones, they are likely to do the same. In "trout water," such a pool always has a riffle or rapid at its head, and just below this the water is cooler and has more oxygen than ordinary. Gill-breathing is much easier in fishes facing upstream. Also, in such position, the fish can readily snap up any edibles coming down with the current. These would seem to explain, in part at least, the heads-upstream of this regiment of trout.

At first glance, in Plate I, Fig. 2, we see scores of trout in right-left ranks—fishes on parade—and the ranks separated by right-left stretches of gravel swept clean of fine detritus. Now let us recall that Mr. Atlee found ranked trout in the stream leading into the Bay of Chaleur, Gulf of St. Lawrence, maintaining their positions by moving their tails right and left in unison. Also Dr. Perry saw marine fishes at Naples, southwest coast

of Florida, acting in similar fashion. So we must conclude that the trout in Plate I, Fig. 2, were doing this very thing. Any given rank of trout fans out the fine detritus under the tails of its members. This is checked and some of it precipitated by the bodies of the rank of fishes just behind it—and so all the way from the foremost rank to the hindmost. Probably these rows of trout lie on gently backward sloping ridges of the detritus. This cleaning action holds best for the center of the stream but fades out somewhat on the edges where the current is weaker.

The collecting of data for an article on military fishes was begun more than 20 years ago. But the work went slowly and presently press of other work—particularly the editing of the Bashford Dean Memorial Volume—led to the filing away of all material till a more convenient time—which has just come. During this period of inactivity in this study, letters came in from a few persons who had heard of my interest in this problem. But their statements were in very general terms, and quite unclear. Had I taken the time to ask for more specific accounts of what they saw, I might have gotten additional valuable data. Now it is too late.

However, abundant evidence is to be found in the written accounts and in the sketches and photographs herein to establish the fact that various fishes, but especially trout, do rank themselves in parade order. These data certainly justify the title of this article. For trout in running water, some tenable explanation has been advanced. But for trout and all other fishes, where behavior has been described, there must be a more fundamental universal reason. This no one has attempted —the explanation must be left to the animal behaviorists.

Finally, it may be said that, from the comments of several friends, who know of the work on this article, I am satified that this curious behavior of ranked fishes, "fishes on parade," is not at all uncommon. In fact, it is probably far better known than the present writer realizes. However, it is a curious thing that in this study there has not been found a single article with such an indicative title as this paper bears and it is hoped that others, who have witnessed this curious behavior, will publish their observations and thus establish this parade behavior as a normal procedure.

## EXPLANATION OF THE PLATE.

### Plate I.

Fig. 1. Ranked trout in a pool at Rotorua, New Zealand. Discounting the shadows, the trout are seen to be roughly ranked in pairs. Photograph by Howard B. MacDonald.

Fig. 2. Resting trout in eight ranks, like soldiers on parade, photographed in the Brule River, 40 miles from Duluth, Minnesota. From Field & Stream, 1929.

FIG. 1.

FIG. 2.

FISHES THAT RANK THEMSELVES LIKE SOLDIERS ON PARADE.

# 11.

## Notes on Seasonal Changes in *Creatophora cinerea,* the Wattled Starling.

LEE S. CRANDALL.

(Plate I).

The Wattled Starling (*Creatophora cinerea*), is an African member of the family Sturnidae. It has a rather wide distribution, extending from southwestern Arabia through East Africa to the Cape. An investigation of seasonal changes in males of this species is outlined in the following notes.

### SEQUENCE 1.

A young specimen of the Wattled Starling (*Creatophora cinerea*) of undetermined sex, and unknown locality, was received at the New York Zoological Park on October 17, 1927.

During the entire period of observation this bird, as well as the others noted, was kept in an indoor, heated aviary from October to May, with access to an outdoor cage during the intervening months.

At the time of arrival, the head and throat were completely feathered and only the usual narrow, bare malar streaks were visible.

In the spring of 1928, the bird showed itself to be a male by an enlargement of the throat wattle, although there was no evidence of crown wattles and no loss of plumage of the head.

In the spring of 1929, the throat wattle again became enlarged, a small area of the forehead became bare and the crown wattles appeared, reaching an upright maximum of about ⅛".

On April 19, 1930, the feathers of the forehead were dropping out. By May 9, the crown and face were black and entirely bare, except for a small tuft behind each nostril. The occipital region was bare and yellow.

The crown wattles, completely sessile, had no power of erection. The posterior wattle, attached longitudinally, measured 9 mm. at the base, expanding to a width of 11 mm. and reaching a length of 20 mm. The anterior wattle, set at an approximate right angle to the longitudinal center line, overhung the base of the bill and was overhung, in turn, by the posterior wattle. Its width at the base was 7 mm., its greatest width was 15 mm. and its greatest length 11.5 mm.

The throat wattle, along the anterior margin, measured 40 mm. when drawn out with the fingers. (As this wattle is slightly retractile, an accurate measurement could not be made.) It is bifurcated at the tip, the right division measuring 9 mm., the left 12 mm.

At this time, the bird indulged in mild courtship maneuvers, tossing his head so that the crown wattles might fall on one side or other, and singing a broken and guttural song.

On August 25, the wattles were seen to be shrinking and feathers of head and face growing. This process continued until, on September 14, the wattles were entirely withdrawn and feathering was complete. However, the nodular crown wattles, normally invisible, remained discernible when the plumage was tightly compressed. Also, the malar streaks, from which the throat wattle had sprung, remained slightly more pronounced than in an immature male or a female.

During the following years, changes took place as follows:

1931. April 11. Feathers dropping.
May 2. Change complete.
September 26. Feathers growing.
October 17. Change complete.

1932. March 1. Feathers dropping.
March 22. Change complete.
September 19. Head feathering, wattles shrinking.
October 10. Change complete.

1933. January 4. Feathers dropping.
January 25. Change complete.
August 18. Head feathering.
September 12. Change complete.
December 1. Feathers dropping.
December 26. Change complete.

1934. September 12. Head feathering.
October 1. Change complete.

1935. February 27. Feathers dropping.
March 22. Change complete.
September 30. Head feathering.
October 22. Change complete.
December 30. Feathers dropping.

1936. January 13. Change complete.
January 20. Feathers re-growing, wattles shrinking.

February 3. Head entirely re-feathered, wattles partly retracted.
February 10. Feathers dropping again, wattles enlarging.
February 24. Change complete, wattles fully extended, bird singing.
September 21. Feathers growing.
October 14. Change complete.
December 21. Feathers dropping.

1937. January 8. Change complete.
September 20. Feathers growing.
October 7. Change complete.
December 20. Feathers dropping.

1938. January 3. Change complete, wattles fully enlarged.
February 7. Feathers re-growing, wattles shrinking.
February 21. Feathering complete.
March 7. Feathers dropping again, wattles enlarging.
March 28. Change complete.
September 12. Feathers growing.
October 1. Change complete.
December 19. Feathers dropping.

1939. January 6. Change complete.
March 5. Observations ended by death of subject.

SEQUENCE 2.

Two Wattled Starlings which proved to be males, were received on December 14, 1934, from a dealer. The locality from which they had come was unknown. These birds were kept together, under identical conditions, during the course of the following observations. They are designated as #1 and #2. Both were fully feathered on arrival.

1935. #1. May 1. Feathers dropping.
May 21. Change complete, crown and throat wattles well developed.
October 21. Feathers growing, wattles shrinking.
November 13. Change complete.

#2. June 5. Throat wattle enlarged, feathers dropping.
June 24. Face and crown bare, throat wattle pendant, no evidence of crown wattles.
October 28. Feathers growing.
November 11. Change complete.

1936. #1. April 6. Feathers dropping.
April 26. Change complete.
October 26. Feathers growing.
November 13. Change complete.

#2. April 27. Feathers dropping.
May 16. Change complete, crown wattles minute.
November 2. Feathers growing.
November 20. Change complete.

1937. #1. March 15. Feathers dropping.
March 31. Change complete.
October 18. Feathers growing.
November 6. Change complete.

#2. April 12. Feathers dropping.
April 29. Change complete, crown wattles minute, throat wattle deeply pendant.
October 25. Feathers growing.
November 14. Change complete.

1938. #1. February 28. Feathers dropping.
March 16. Change complete.
October 31. Feathers growing.
November 18. Change complete.

#2. March 28. Feathers dropping.
April 18. Change complete, crown wattles minute.
October 2. Feathers growing.
October 21. Change complete.

1939. #1. March 6. Feathers dropping.
March 25. Change complete.
October 23. Feathers growing.
November 10. Change complete.

#2. March 20. Feathers dropping.
April 7. Change complete, crown wattles minute.
October 23. Feathers growing.
November 15. Change complete.

1940. #1 February 26. Feathers dropping.
March 15. Change complete.
September 23. Feathers growing.
October 9. Change complete.

#2 April 8. Face feathers dropping.
April 27. Change complete, crown wattles minute.
October 28. Feathers dropping.
November 13. Change complete.

1941. #1. March 3. Feathers dropping.
March 23. Change complete.
October 13. Feathers growing.
October 29. Change complete.

#2. April 14. Feathers dropping.
May 4. Change complete, crown wattles minute.
October 27. Feathers growing.
November 14. Change complete.

1942. #1. March 9. Feathers dropping.
March 31. Change complete.
September 28. Feathers growing.
October 19. Change complete.

#2. March 30. Feathers dropping.
April 20. Change complete, crown wattles minute.
November 9. Feathers growing.
November 29. Change complete.

1943. #1. February 15. Feathers dropping.
March 8. Change complete.

#2. March 15. Feathers dropping.
April 7. Change complete.

SEQUENCE 3.

Two Wattled Starlings which appeared to be male and female, were purchased from Christoph Schulz on August 9, 1935. They were reported by Schulz to have been collected in Kenya. The male was in breeding condition at the time of arrival, with head bare and wattles well developed.

Throughout the course of observations on this pair, the female showed no plumage change and no enlargement of the bare malar streaks, at the time the male was coming into breeding condition. During October and November of each year she went through a complete body molt.

Changes in the male were noted as follows:

1935. October 22. Feathers growing.
November 13. Change complete.

1936. April 6. Feathers dropping.
April 24. Change complete, wattles well developed.
October 5. Feathers growing.
October 27. Change complete.

1937. January 18. Feathers dropping.
February 4. Change complete.
March 1. Feathers re-growing.
March 15. Face almost completely feathered, wattles shrunken.
March 22. Feathers dropping again, wattles re-enlarging.
April 2. Head entirely bare, wattles large.
October 25. Feathers growing.
November 12. Change complete.

1938. February 14. Feathers dropping.
March 3. Change complete but wattles small.
March 28. Face re-feathering.
April 11. Face almost entirely re-feathered.
April 18. Feathers dropping again.
May 5. Change complete, wattles much enlarged.
October 31. Face feathers growing.
November 19. Change complete.

1939. March 27. Feathers dropping.
April 17. Change complete.
October 9. Feathers growing.
October 30. Change complete.

1940. February 26. Feathers dropping.
March 20. Change complete.
September 23. Feathers growing.
October 10. Change complete.

1941. March 24. Feathers dropping.
April 12. Change complete.
September 29. Feathers growing.
October 18. Change complete.

1942. March 2. Feathers dropping.
March 20. Change complete.
October 5. Feathers growing.
October 23. Change complete.

1943. February 15. Feathers dropping.
March 6. Change complete.

## Summary.

Seasonal changes in four male and one female specimens of the Wattled Starling (*Creatophora cinerea*) have been tabulated and described. All of these birds were kept under identical conditions, as far as caging, food and temperatures were concerned. It is shown that in the males there is a seasonal loss of the plumage of the head, accompanied by enlargement of the crown and throat wattles. The single female showed no enlargement of the bare gular tracts and had only a single annual change of plumage, which took place at the period of regression in the accompanying male.

The males of Sequence 1 and Sequence 3 showed occasional "false starts," in which newly bared heads almost immediately re-feathered, quickly followed by a resumption of the bare condition. Neither of the two males described in the second series of observations showed this phenomenon.

Recorded dates of changes were established on a visual basis. However, standards of judgement were the same in all cases, so that periods indicated are properly comparable and variations would be small.

February 3. Head entirely re-feathered, wattles partly retracted.
February 10. Feathers dropping again, wattles enlarging.
February 24. Change complete, wattles fully extended, bird singing.
September 21. Feathers growing.
October 14. Change complete.
December 21. Feathers dropping.

1937. January 8. Change complete.
September 20. Feathers growing.
October 7. Change complete.
December 20. Feathers dropping.

1938. January 3. Change complete, wattles fully enlarged.
February 7. Feathers re-growing, wattles shrinking.
February 21. Feathering complete.
March 7. Feathers dropping again, wattles enlarging.
March 28. Change complete.
September 12. Feathers growing.
October 1. Change complete.
December 19. Feathers dropping.

1939. January 6. Change complete.
March 5. Observations ended by death of subject.

SEQUENCE 2.

Two Wattled Starlings which proved to be males, were received on December 14, 1934, from a dealer. The locality from which they had come was unknown. These birds were kept together, under identical conditions, during the course of the following observations. They are designated as #1 and #2. Both were fully feathered on arrival.

1935. #1. May 1. Feathers dropping.
May 21. Change complete, crown and throat wattles well developed.
October 21. Feathers growing, wattles shrinking.
November 13. Change complete.

#2. June 5. Throat wattle enlarged, feathers dropping.
June 24. Face and crown bare, throat wattle pendant, no evidence of crown wattles.
October 28. Feathers growing.
November 11. Change complete.

1936. #1. April 6. Feathers dropping.
April 26. Change complete.
October 26. Feathers growing.
November 13. Change complete.

#2. April 27. Feathers dropping.
May 16. Change complete, crown wattles minute.
November 2. Feathers growing.
November 20. Change complete.

1937. #1. March 15. Feathers dropping.
March 31. Change complete.
October 18. Feathers growing.
November 6. Change complete.

#2. April 12. Feathers dropping.
April 29. Change complete, crown wattles minute, throat wattle deeply pendant.
October 25. Feathers growing.
November 14. Change complete.

1938. #1. February 28. Feathers dropping.
March 16. Change complete.
October 31. Feathers growing.
November 18. Change complete.

#2. March 28. Feathers dropping.
April 18. Change complete, crown wattles minute.
October 2. Feathers growing.
October 21. Change complete.

1939. #1. March 6. Feathers dropping.
March 25. Change complete.
October 23. Feathers growing.
November 10. Change complete.

#2. March 20. Feathers dropping.
April 7. Change complete, crown wattles minute.
October 23. Feathers growing.
November 15. Change complete.

1940. #1 February 26. Feathers dropping.
March 15. Change complete.
September 23. Feathers growing.
October 9. Change complete.

#2 April 8. Face feathers dropping.
April 27. Change complete, crown wattles minute.
October 28. Feathers dropping.
November 13. Change complete.

1941. #1. March 3. Feathers dropping.
March 23. Change complete.
October 13. Feathers growing.
October 29. Change complete.

#2. April 14. Feathers dropping.
May 4. Change complete, crown wattles minute.
October 27. Feathers growing.
November 14. Change complete.

1942. #1. March 9. Feathers dropping.
March 31. Change complete.
September 28. Feathers growing.
October 19. Change complete.

#2. March 30. Feathers dropping.
April 20. Change complete, crown wattles minute.
November 9. Feathers growing.
November 29. Change complete.

1943. #1. February 15. Feathers dropping.
March 8. Change complete.

#2. March 15. Feathers dropping.
April 7. Change complete.

SEQUENCE 3.

Two Wattled Starlings which appeared to be male and female, were purchased from Christoph Schulz on August 9, 1935. They were reported by Schulz to have been collected in Kenya. The male was in breeding condition at the time of arrival, with head bare and wattles well developed.

Throughout the course of observations on this pair, the female showed no plumage change and no enlargement of the bare malar streaks, at the time the male was coming into breeding condition. During October and November of each year she went through a complete body molt.

Changes in the male were noted as follows:

1935. October 22. Feathers growing.
November 13. Change complete.

1936. April 6. Feathers dropping.
April 24. Change complete, wattles well developed.
October 5. Feathers growing.
October 27. Change complete.

1937. January 18. Feathers dropping.
February 4. Change complete.
March 1. Feathers re-growing.
March 15. Face almost completely feathered, wattles shrunken.
March 22. Feathers dropping again, wattles re-enlarging.
April 2. Head entirely bare, wattles large.
October 25. Feathers growing.
November 12. Change complete.

1938. February 14. Feathers dropping.
March 3. Change complete but wattles small.
March 28. Face re-feathering.
April 11. Face almost entirely re-feathered.
April 18. Feathers dropping again.
May 5. Change complete, wattles much enlarged.
October 31. Face feathers growing.
November 19. Change complete.

1939. March 27. Feathers dropping.
April 17. Change complete.
October 9. Feathers growing.
October 30. Change complete.

1940. February 26. Feathers dropping.
March 20. Change complete.
September 23. Feathers growing.
October 10. Change complete.

1941. March 24. Feathers dropping.
April 12. Change complete.
September 29. Feathers growing.
October 18. Change complete.

1942. March 2. Feathers dropping.
March 20. Change complete.
October 5. Feathers growing.
October 23. Change complete.

1943. February 15. Feathers dropping.
March 6. Change complete.

## Summary.

Seasonal changes in four male and one female specimens of the Wattled Starling (*Creatophora cinerea*) have been tabulated and described. All of these birds were kept under identical conditions, as far as caging, food and temperatures were concerned. It is shown that in the males there is a seasonal loss of the plumage of the head, accompanied by enlargement of the crown and throat wattles. The single female showed no enlargement of the bare gular tracts and had only a single annual change of plumage, which took place at the period of regression in the accompanying male.

The males of Sequence 1 and Sequence 3 showed occasional "false starts," in which newly bared heads almost immediately re-feathered, quickly followed by a resumption of the bare condition. Neither of the two males described in the second series of observations showed this phenomenon.

Recorded dates of changes were established on a visual basis. However, standards of judgement were the same in all cases, so that periods indicated are properly comparable and variations would be small.

## EXPLANATION OF THE PLATE.

### Plate I.

Fig. 1. Adult ♂ Wattled Starling (Sequence 1), photographed on June 13, 1933. The head is completely bare and wattles fully developed.

Fig. 2. The same bird, photographed on November 20, 1934. He has completed regressive changes and is in resting condition. The nodular crown wattles, not normally visible at this time, are seen because the feathers are tightly compressed. The throat wattle has receded to the lateral malar patches.

FIG. 1.

FIG. 2.

NOTES ON SEASONAL CHANGES IN CREATOPHORA CINEREA, THE WATTLED STARLING.

# 12.

## Insect Migration at Rancho Grande in North-central Venezuela. General Account.[1]

WILLIAM BEEBE.

*Director, Department of Tropical Research, New York Zoological Society.*

(Plates I & II; Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

CONTENTS.



[1] Contribution No. 843, Department of Tropical Research, New York Zoological Society.

### GENERAL ACCOUNT.

Throughout the first year of our occupation of the station at Rancho Grande in north-central Venezuela, we had no idea of the importance of Portachuelo Pass as a migration flyway for birds and insects. Even later on, when we came to compile a list of thirteen life zones within our visual radius, a fourteenth, the Aerial Zone, was added with hesitation, having in mind the inclusion of organisms such as hummingbirds, swifts and mayflies which spend the major part of their lives in midair. Almost immediately, however, the value of and need for such a niche in our phenological program became apparent.

If for no other reason, an Aerial Zone was needed to accommodate the volant organisms which passed and repassed, or occasionally were detected soaring in air, and which were never to be found resting or flying in the jungle of our immediate area of research. Many of these creatures were essentially tropical, occupying our subtropical elevation only as a temporary route of passage.

About 200 meters beyond Rancho Grande, the road leads through a narrow notch in the east-west, coastal Andean range. This is Portachuelo Pass with an elevation of 1,136 meters, about 36 meters higher than Rancho Grande. The flattened floor of the pass is only about 20 meters wide, and the shoulders on either side rise in sharp ridges, 389 meters to the summit of Pico Periquito on the west, and 764 meters on the east to the top of Pico Guacamayo.

The pass is at the 22.5 kilometer mark on the road from Maracay, and, as has been stated, is at an elevation of 1,136 meters. Kilometer 31, well to the north of the pass, is 770 meters above the sea. Kilometer 15, equally distant to the south of the pass and close to the beginning of the lowland savannas, is 760 meters above the sea. At both of these lower stations many migrants have been taken, en route to or on their way from the pass.

The pass is on the real divide, shunting the waters on its northern slope into the

Caribbean Sea, and those on the south side ultimately into Lake Valencia.

Fifteen orders of insects have already been collected or observed as they passed southward on migration, singly, in few or in enormous numbers. Of other possible migrants this leaves only three orders, Ephemerida, Embiidina and Trichoptera. The four parasitic groups, Anopleura, Siphonoptera, Mallophaga and Strepsiptera, are of course absent, although the two latter doubtless hitch-hike through the pass on birds and bees respectively.

The migrating orders, arranged in three columns of relative numbers, are as follows:

| *Rare* | *Moderate* | *Abundant* |
|---|---|---|
| Isoptera | Orthoptera | Coleoptera |
| Neuroptera | Odonata | Lepidoptera |
| Plecoptera | Homoptera | Diptera |
| Corrodontia | Hemiptera | Hymenoptera |
| Thysanoptera | | |
| Dermaptera | | |
| Mecoptera | | |

Up to the date of this publication, Mr. Henry Fleming has identified two hundred and forty-five species of butterflies, and fifty-two species of day-flying moths. Of the single family of nocturnal moths, Sphingidae, we have recorded seventy-six species, either directly migrating through the pass, or flying about our lights at Rancho Grande. Mr. Fleming has found only two of these which may be classed as breeding in the cloud forest surrounding the pass and our laboratory.

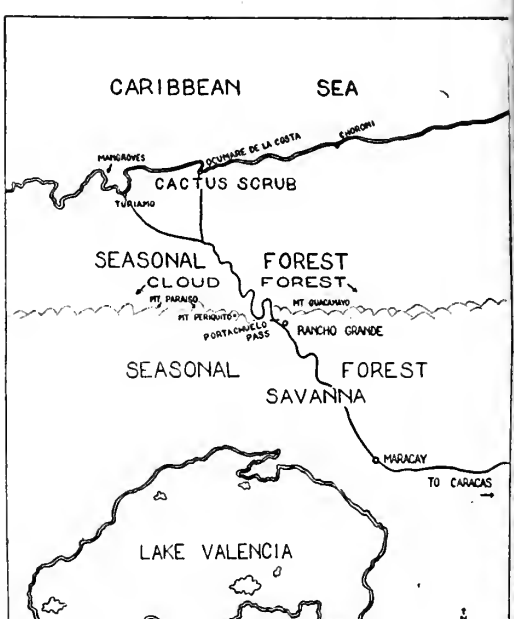
Except for a temporary, limited, northward drift of individual *Phoebis* (*Catopsilia*) in the early part of the rains, the movement of all orders of insects was invariably from north to south through the pass.

## Migrating Insects.

Examples of extremes in migration will serve to point up succeeding papers dealing with families and species.

On April 29, 1946, I caught a solitary butterfly at the rim of the pass. Its wing spread was small, and it was an inconspicuous purplish-brown with five spots of dull white near the tip of each fore wing. It belonged to the family Nymphalidae. I gave it the reference field name of Ten-spot Brown and later found its technical name was *Eunica monima* (Cramer).

On May 4, five days later, I caught sight of several butterflies passing overhead and at the pass itself I entered a dense swarm of the Ten-spots. Mingled with them were tailed nymphalids, *Marpesia chiron chiron* (Fab.) in large numbers, and now and then a swarm of large sulphurs, *Phoebis eubule marcellina* (Cramer). In the distance I could see myriads of Ten-spots converging on the pass. One swoop of the net captured seven, five of which were tattered and torn, the remaining two freshly emerged.




Text-fig. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

Two of us climbed a mound giving a view of about half the width of the pass, and here, facing in opposite directions, at eye level, we averaged thirteen hundred butterflies in several counts of four minutes each. At intervals throughout an hour and a half this insect content of a limited time and space remained fairly constant, and when we left we knew that at the very least, two hundred and eighty-six thousand Ten-spots had passed close to us. An hour later the insects were going full strength and now I brought to bear my giant binoculars, first twelve and then twenty powers. I began about twenty-five feet overhead and then refocussed slowly upward until the limit of vision of the small insects was reached. This, judged by horizontal tests of objects of similar size would be about a half mile zenithwards, and at every fractional turn of the screw, more and more smaller-appearing butterflies fluttered into clarity.

Throughout the entire extent of verticality there was no lessening of denseness of flying insects, and it was almost a pure culture of *Eunica* and *Marpesia*. For many days this particular phase of migration continued, millions upon millions coming from some unknown source, travelling due south to an equally mysterious destination.

Three weeks later, on May 24, there was a resurgent migration of the same species, all fresh insects. Their numbers far exceeded the first wave. Four of us lined up across the entire width of the pass, with stop-watches and counters, completely failed

to keep up with fast enough estimate of numbers, but at the minimum clocked a thousand a second going past in the face of a gentle breeze. In the narrow trail above the gorge it was necessary to put on glasses, so dense were the crowds impinging upon our faces.

As the other extreme, I may mention a half hour of collecting when many species in fewer numbers were passing. Twenty successive specimens of butterflies resolved into eleven species of pierids. On another occasion thirteen individual butterflies proved to be thirteen separate species of ithomiids.

Non-recognition of the pass as a flyway accounts for the small number of observations in the year 1946, and the still more meagre and casual notes in 1945. Some time passed before we realized that all of the host of moths which came in windrows to the roof lights and laboratory windows of Rancho Grande were Portachuelo Pass migrants, deflected by confusion of fog or rain. On clear nights of star and moonlight our torches and portable ultra-violet machines revealed unbroken streams of moths of all sizes headed up and through the pass. Other indirect evidences were the wings, belonging to great numbers of species and individuals of moths, found glued in early morning to the dew-moistened leaves of shrubs and weeds in the pass; the remains of nocturnal feasts of marauding bats.

## Migration Factors.

One definite factor, which seems the dominant stimulus of migration, is the advent of the rainy season. For example, in 1948, there was no hint whatever of migration in February. On March 1 a single torn and bedraggled nymphalid, *Marpesia chiron chiron*, struggled up to the pass and into my net. Hardly another insect appeared for two weeks, throughout a period mostly cold and overcast. Then, on March 15, a day of warm sun after several days of heavy rain, we caught or recorded twenty species of butterflies in considerable numbers. Succeeding weeks of cold resulted in a complete dearth or mere scattering of insects, until April 15. From this date until August 1 there was no cessation of numbers pouring through, varied only by irregular fluctuations due to occasional days of cold rain or very high wind.

September 9 is the latest date of any of our three years of residence, and on that day migration was in full swing. From what I can learn, the passing insects gradually decrease throughout the succeeding two weeks. On the authority of Dr. Francisco Fernandez, Venezuelan Government Entomologist, diurnal migration at the pass ceased for the year by October 1. The annual picture thus seems clear cut.

The following applies more particularly to diurnal Lepidoptera, but in general is true of all orders:

Inhibiting Conditions: Very high winds, from twenty-five miles per hour upward; chilly temperatures, 62° Fahr. down; dense fog (neblina) or heavy rain; darkness.

Favoring Conditions: Calm, up to a twenty mile per hour following wind; 64° Fahr. plus; sun or thin neblina.

Recurrent Waves: These last from twenty minutes to three weeks, and usually comprise few species (two to twenty), but often large numbers of individuals. These waves are occasionally independent of favorable conditions, the hosts of insects banking up in the lee of brush, waiting for good flying weather.

Between Waves: At these times insects tend to fly singly, and in great variety of species.

Wing Condition: Worn and fresh specimens may be present in the same wave, but as a rule all are worn or all are freshly emerged.

Models and Mimics: Some of the more generally accepted categories of models and mimics may appear mingled together in the waves, or, very interestingly, there are not infrequently pure cultures of each, confined to waves of considerable magnitude.

Specific Characteristics: Normal specific characteristics of flight and of choice of habitat are maintained throughout migration. Rapid or slow flyers do not alter their relative speeds, nor change their dodging, zigzag or direct flight. The same applies as well to high or low habitual levels of flight, fast or slow flapping of wings. Species which prefer to wind their way through low, thick brush adhere to this habit en route up to and through the pass.

Sexes and Breeding: The general rule is the presence of both sexes, and many of the females captured alive deposit eggs within twenty-four hours. Rarely, attempts at mating on migration are observed, or pairs appear to be fighting as they circle rapidly in midair. Very few loiter to feed at blossoms. Few worn individuals stop to rest.

Diurnal Sequence: A few insects, belonging to various orders other than Lepidoptera, appear very early in the morning, for months on end, flying past singly, but in the aggregate in great numbers. Especially noticeable among these are two species of cockchafers (*Cyclocephala* spp.), a chrysomelid (*Diabrotica quindecimpunctata*), a small vespid (*Stalopolybia areata*), a giant hairy scoliid (*Campsomeris ianthina*), and a bee (*Euglossa fasciata*). The numbers of these solitary migrants passing on the morning of June 19, 1948, typifies the numbers on every day for the preceding two months: cockchafers, 200; chrysomelids 150; small vespids 150; giant scoliids 140; rufous bees 90.

Following these there comes, for an hour or longer, a steady procession of day-flying moths, also singly. Butterflies dominate the remainder of the day as far as relatively large insects are concerned. Throughout the

daylight hours there is a continuous passing of migration nekton, hosts upon hosts of minute winged insect life. When dusk gives way to darkness, moths and other nocturnal insects appear, and surge through the pass. If the night is fine, with clear moon or starlight, all continue down Limon Gorge. If the sky is overcast, thick with neblina or rain, the moths leave their direct southern route and detour in tens of thousands to our lighted laboratory windows or white roof walls.

Interpretation: At present, before a detailed study has been made of the mass of specimens and data, and further explorations undertaken of places of origin and destination in surrounding country, no reasonable explanation of this wholesale annual emigration is possible.

Unlike the migration of hosts of *Phoebis* males which I have observed in British Guiana and elsewhere, the Portachuelo hosts are represented by both sexes. Many of the females are ready to deposit eggs, although they are headed away from areas rich in a variety of plants, toward less luxuriant savannas.

The known distribution of many species, or especially subspecies, of butterflies such as the Papilios, shows that their place of origin cannot be very far away to the north and west, but as yet we have no hint of whence the fifteen orders are derived, or whither they are headed. From our own observations, reinforced by the reports of reliable govenment official entomologists, we are certain that little or no migration occurs during the dry season, and that not an insect ever returns to its natal haunts. Hence the phenomenon is really an emigration of the cross section of a considerable volant invertebrate fauna of this part of Venezuela.

Observations during three years confirm the fact that this migration is a regular annual event. It presents the inexplicable problem of a regular abstraction of an appreciable percentage of non-returning population from the area of origin. This implies the leaving behind of an adequate residual number of non-migrants to carry on the race and to sustain future migration.

Sight Identification: When there came recognition of migration on a relatively great scale, our first and indeed continued impulse was to capture as many specimens of as many different kinds as was humanly possible. On an early day of observation a butterfly was taken which, in our mind, was instantly labelled a Monarch, *Danias archippus*, or, if you prefer, *Danaus plexippus*, a familiar of our northern fields. Within an hour eighteen of the same species flapped slowly past, two of them alighting for a few seconds. Within ten minutes there passed eight smaller, darker red butterflies, two of which we took, which vividly reminded us of our northern *Danaus berenice*, commonly called the Queen. Ultimately these two resolved into *Danaus plexippus megalippe* and *Danaus eresimus eresimus*, but throughout my notes, before identification, they were nostalgically recorded as Monarch and Queen. The important thing is that, being easily and accurately recognizable at a distance in flight for what they are, I am able to record, without fear of error, all the numbers that came within my purview, in all my hours of observation at the pass.

This is all by way of introducing the important question of sight identification, which, in any research such as the present, must play a dominant part. I based all my field naming first, on captured and ultimately precisely named specimens, and secondly, on characters in flying or resting insects which left no shadow of doubt. Although hundreds and tens of thousands of insects passed with only the vaguest hints of family or genus, yet day after day familiarity introduced to the perception characteristics of flight, pattern, color and shape of wings, and general facies, which materially increased range and certainty of recognition.

Viewing from a distance of ten meters, groups of species mounted in open cases, proved an excellent check on visual awareness of distinctions. A brief treatment of sight identification will be added to each paper dealing with families of insects.

This and following papers are intended only as factual presentations of notes made during three seasons of observations of migration from north to south through Portachuelo Pass. Hence no attempt has been made at correlation or even mention of migrations of the same or related species observed by entomologists elsewhere. The insects themselves will be considered group by group in successive papers, with a final summary in detail of the migration as a whole.

We hope, in future expeditions in this same field, that data will be obtained which will clarify the place of origin and ultimate destination of the insect hosts, as well as the initiating stimuli and directive factors of their migration.

An account of the bird migration through the pass has already appeared, treating of sixty species divided among ten types of migration.[2]

## EXPLANATION OF THE PLATES.

### Plate I.

Fig. 1. Looking south toward Portachuelo Pass from Kilometer 31.

Fig. 2. Portachuelo Pass, the notch in the distant sky-line, from farther north, near the sea.

### Plate II.

Fig. 3. Migrant insects alive but quieted by refrigeration.

Fig. 4. Migrant moths deflected in great numbers, on nights of storm, from their migration through the pass, to the electric lights on Rancho Grande roof.

[2] *Zoologica*, 32 (18), 1947, pp. 153-168.

FIG. 1.

FIG. 2.

INSECT MIGRATION AT RANCHO GRANDE IN NORTH-CENTRAL VENEZUELA.
GENERAL ACCOUNT.

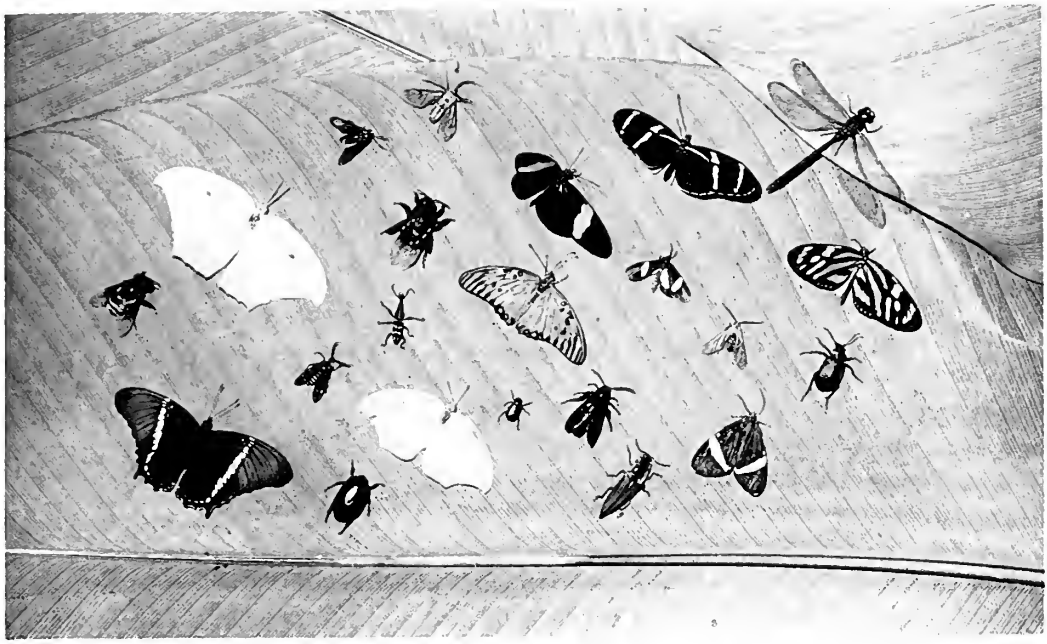


FIG. 3.

FIG. 4.

INSECT MIGRATION AT RANCHO GRANDE IN NORTH-CENTRAL VENEZUELA.
GENERAL ACCOUNT.

# 13.

## The Behavior of Two Captive Specimens of the Lowland Gorilla, *Gorilla gorilla gorilla* (Savage & Wyman).[1]

B. F. RIESS,[2] SHERMAN ROSS,[3] S. B. LYERLY,[4] AND H. G. BIRCH.[5]

*Behavior Research Fellows* (1948), *New York Zoological Society.*

(Plates I & II; Text-figures 1 & 2).

### I. INTRODUCTION.

The field of comparative behavior research has long been subject to two methodological factors which have to a certain extent prevented the attainment of its goal, namely the securing of information on behavioral processes of representative species of a wide range of living organisms. The first factor has been the concentration of research workers on those animals which are adaptable to the limited conditions of laboratories. This emphasis on a few selected species has led to the second factor, the acceptance of the conventional laboratory as the prototype of habitat for the species under investigation. Both these methodological limitations have arisen in part from the same set of circumstances, the relative lack of availability of less adaptable organisms and the expense of field studies. The increasing number of investigations under naturalistic field conditions and of studies on rare specimens under favorable conditions has provided additional evidence of the fruitfulness of the extension of both laboratory and field methodology to specimens other than those generally used in comparative behavior laboratories.

It is one of the purposes of this paper to point to a source of data which can facilitate not only the collection of more information on a wider variety of animals but which can also serve as a training facility for field-workers and others. Within the reach of researchers in most large cities there exist collections of living animals in great variety of species and under varied living conditions. The reference is to the zoological parks and exhibition areas. In many of these, natural habitat conditions are approximated and even the differences can be fertile sources of comparative psycho-ecological studies.

In 1937, Carpenter (2) published a study of two young male mountain gorillas, *Gorilla gorilla berengei*, resident at the San Diego Zoo. In this paper he pointed to the opportunities presented by the fourteen specimens of the largest of the great apes which he listed as available in the zoological parks of the world. Gorillas offer a dramatic field for this type of research since they are, with the exception of the orang-utan, the least studied of the anthropoid apes. The present paper seeks to compare Carpenter's data with those obtained in a study of male and female pre-adolescent lowland gorillas, *Gorilla gorilla gorilla*, in the New York Zoological Park (Bronx Zoo). Such comparative data as can be assembled will be helpful to workers who seek a base line for similar investigation elsewhere. That these investigations are possible is demonstrated in Table I which lists the location and over-all biological indices of the specimens now resident in various collections. The number of gorillas in the United States is increasing. In 1937 there were only eight specimens in this country; today there are twenty-four.

Other than Carpenter's study, material on the behavior of the gorilla is found only in a limited number of papers. Yerkes' pioneer work (6) with the pre-adolescent female mountain gorilla, Congo, is known to all students of comparative psychology. Bingham's 1932 observations (1) on gorillas in their native habitat and Valker's similar study in the Gaboons (5) in 1931 are the only other relevant research. The two lowland gorillas in the New York Zoological Park are included in a report of the external genitalia published by Goss (3).

### II. SUBJECTS.

The gorillas studied at the Bronx Zoo are Oka, female, and Makoko, male. Since this study was made the Bronx Zoo has acquired a young female mountain gorilla, but no reference to it will be made in this report, except to list it in Table I. Little is known of the early history of Oka and Makoko. Both animals arrived in the Zoo on September 7, 1941, at which time they weighed 20 and 28

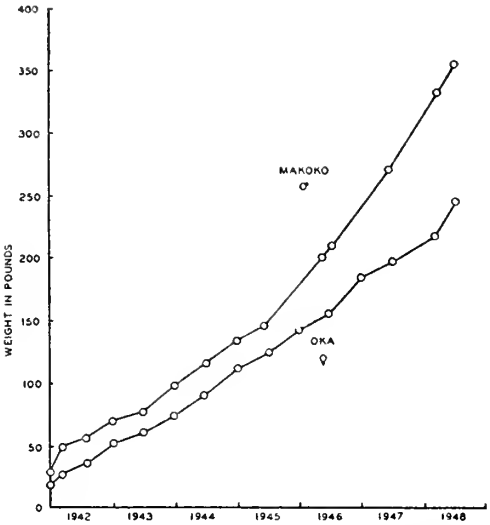
1 The success of this project was due in large part to the co-operation of the staff and keepers of the New York Zoological Park. Particular thanks are due Mr. Fairfield Osborn, Mr. John Tee-Van, Mr. Lee S. Crandall, Dr. L. J. Goss, Keepers Reilley and Quinn, and Mr. Sam Dunton, photographer.

2 Hunter College of the City of New York, N. Y. C.

3 Bucknell University, Lewisburg, Penna.

4 University of North Carolina, Chapel Hill, N. C.

5 City College of New York, N. Y. C.




TEXT-FIG. 1. Rate of growth of Oka and Makoko from time of arrival at the New York Zoological Park on September 7, 1941, until summer of 1948.

pounds respectively. Ages were estimated as one and three years on the basis of weight and bone structure. Text-figure 1 gives the data on the growth of the specimens from the time of arrival until the summer of 1948. The female was weighed, up to June, 1948, while on the keeper's back, the male's weight being merely estimated. In 1948 a Toledo balance was installed, on which the animals were weighed when they voluntarily mounted a platform.

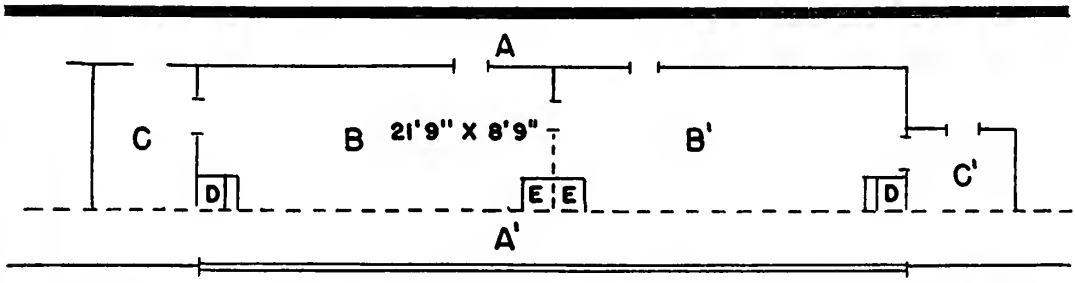
At the present time, Oka and Makoko are magnificent specimens. Makoko has a particularly brilliant coat and a notably prominent supra-orbital ridge. Oka is less impressively marked but is a splendid female example of the species. Both animals are active, healthy and strong. Indeed, Makoko's grip is so powerful that it has been necessary to replace the ¾-inch steel bars of the cage front, which he bent repeatedly. A steel horizontal ladder had to be removed from his cage when he tore it loose from its mooring. Oka is less destructive and retains her ladder.

## III. Environmental Conditions.

The gorillas are housed in individual cages separated by a partition consisting of a solid metal access door and a double grill of steel bars. At the ends of each cage are doors leading to shift cages into which the animals are chased when the exhibition compartments are cleaned or repaired. The back wall of the living space is solid masonry with a recessed access door. Between the glass partition through which the public views the animals and the metal barred cage fronts is a passageway for the keepers. The internal features of the living compartments include a platform and a three-step staircase, with the platforms raised two inches from the floor, facing each other in front of the grill between the two cages. The staircases are at the ends near the shift cages. Oka's cage contains a metal horizontal ladder slung between the rear wall and the cage front at a height of three feet. Text-figure 2 shows the floor plan of the gorilla exhibition space.

## IV. Daily Schedule of Animal Care.

Although the animals are on exhibition during the hours of 10:00 A.M. to 5:00 P.M. (except on Sundays when the visiting time is extended to 6:30 P.M.), the daily routine is more extensive. The overhead fluorescent lights are turned on at 8:00 A.M. when the keepers enter the building. Between 8:30 and 9:00 in the morning, the gorillas, each of whom has been in its own cage all night, are given their morning meal of skimmed milk and raw eggs. The ingredients are mixed and fed to each gorilla by tilting a can containing the mixture into the subject's mouth as the animal protrudes its lips through the bars of the cage front. Some half-hour to three-quarters of an hour later, the keepers move the gorillas to the shift cages. Separation and enclosure in the individual cages are effected by means of a stream of water. With the gorillas out of the way, the cages undergo thorough cleaning. Shortly before visiting time, the animals are released and are frequently permitted to remain together in one of the two cages for periods up to one hour. This opportunity for association occurs five




TEXT-FIG. 2. Floor plan of gorilla compartments in New York Zoological Park. **A**, **A'**, passageways for keepers. **B**, **B'**, exhibition cages for Oka (female) and Makoko (male), respectively. **C**, **C'**, shift cages. **D**, three-step stairs. **E**, platforms; right-hand platform used for weighing. **Thin line** indicates solid wall; **dotted line** indicates grill-front walls; **double line** indicates glass partition.

TABLE I.

Physical Characteristics of Gorillas in the United States.*

| Name. | Location. | Form. | Sex. | Estimated age on September 1, 1949. | Known Weight. | Estimated Weight. |
|---|---|---|---|---|---|---|
| Oka | N. Y. Zool. Park | *gorilla* | F | 9 yrs. | 282 lbs. | |
| Makoko | N. Y. Zool. Park | *gorilla* | M | 11 yrs. | 408 lbs. | |
| Sumaili | N. Y. Zool. Park | *berengei* | F | 20 mos. | 20 lbs. | |
| Joanne | Central Park Zoo, N. Y. C. | *gorilla* | F | 10 yrs. | | 190 lbs. |
| Carolyn | Central Park Zoo, N. Y. C. | *gorilla* | F | 10 yrs. | | 190 lbs. |
| Bamboo | Philadelphia Z. G. | *gorilla* | M | 23 yrs. | | 435 lbs. |
| Massa | Philadelphia Z. G. | *gorilla* | M | 18 yrs. | | 400 lbs. |
| Bushman | Lincoln Park Zoo, Chicago | *gorilla* | M | 21½ yrs. | 542 lbs. | |
| Sinbad | Lincoln Park Zoo, Chicago | *gorilla* | M | 20 mos. | 38 lbs. | |
| Rajah | Lincoln Park Zoo, Chicago | *gorilla* | M | 29 mos. | | 47 lbs. |
| Irvin Young | Lincoln Park Zoo, Chicago | *gorilla* | M | 33 mos. | 52 lbs. | |
| Lotus | Lincoln Park Zoo, Chicago | *gorilla* | F | 43 mos. | | 75 lbs. |
| Miss Congo† | Chicago Z. P. | *gorilla* | F | 16 yrs. | | 325 lbs. |
| Phil | St. Louis Z. P. | *gorilla* | M | 10 yrs. | | 320 lbs. |
| Bobo | St. Louis Z. P. | *gorilla* | M | 2 yrs. | | 44 lbs. |
| Big Boy | Cincinnati Zoo | *gorilla* | M | 3 yrs. | 35¼ lbs. | |
| Albert | San Diego Zoo | *gorilla* | M | 6 mos. | 9¾ lbs. | |
| Bouba | San Diego Zoo | *gorilla* | F | 10 mos. | 12½ lbs. | |
| Bata | San Diego Zoo | *gorilla* | F | 8 mos. | 10¾ lbs. | |
| Phil | Colorado Springs, Col. | *gorilla* | M | 4 yrs. | | 40 lbs. |
| Gargantua | Ringling Bros. Circus | *gorilla* | M | 17 yrs. | 550 lbs‡ | |
| Mtoto | Ringling Bros. Circus | *gorilla* | F | 16 yrs. | 438 lbs.‡ | |

* On October 31, 1949, three young specimens of *Gorilla g. gorilla* arrived in New York. They were a male and a female weighing 12-14 pounds, and a female weighing about 40 pounds. At the time this paper went to press they were still in the hands of Henry Trefflich, an animal dealer.
† Died Sept. 22, 1949.
‡ 1947 weight.

or six times a week and is the only occasion on which the animals are in unrestricted contact with each other. From the time of separation until the main feeding of the day at approximately 2:30 P.M., the gorillas are unattended except insofar as the keepers play with them while passing in front of the cages. The typical afternoon meal consists of carrots, celery, oranges, apples, grapes, bananas, beets, beans, sweet-potatoes, cabbage, onions, cherries and other seasonable fruits and vegetables. All food is fed raw and supplied through the front bars of the cages. Water, *ad lib.*, is available to each animal from a continuously running spigot which empties into a trough running along the back wall of each cage. At 5:30 P.M. the lights are turned out and the gorillas remain unattended until the next morning.

## V. Observational Procedures.

Preliminary study of the gorillas was started at the beginning of May, 1948. One of the writers (B.F.R.) visited the Primate House at the Zoo on two days of each week and observed the gorillas for one hour. The times selected were in the early morning when the keepers placed the two gorillas in one cage, and in the late afternoon, at about 3:30 P.M. following the afternoon meal. At the later time, the animals were in separate cages.

As a result of the work during May and early June, a list was evolved on which both quantitative and qualitative indices of behavior could be noted. The inventory consisted of 42 items divided into five categories: posture and locomotion; eating, drinking and elimination; self-oriented activity (play?); inter-individual behavior; and observer-oriented behavior. The sheets of the check list were divided into 10 columns, each of which was used for a three-minute period of observation during the total 30 minute duration of the observational session. Thus it was possible to arrive at the total amount of each of the 42 types of behavior during the 30-minute period and also to determine the sequence of behavior during the period. Additional space was provided for running comments on the activity of the gorillas and for additional notes.

The observers worked in pairs and rotated the pairing so that a measure of control over reliability of observation was possible. There was joint discussion of the meaning of each term on the check-list so that the observers would agree on how to label the activity observed. The problem of the animal's reaction to the observer was considered and it was decided to standardize the position of the observers. Since the gorillas are a very popular exhibit and attract large crowds of spectators, the public exhibition space was used as the location for the observers who sat in pairs in front of the glass partition opposite

the communicating grill between the two cages.

Because the activity of the gorillas varied considerably with the time of day, the number of visitors, the daily routine and other variables, it was decided to distribute the 30-minute observation periods over the whole working day of the animal. However, since the gorillas were allowed to be in the same cage with one another only in the early morning, there was a greater concentration of sessions between 9:00 and 10:00 A.M. The total number of observations made during these hours was 10 one-half hour periods. Sixty-eight sessions were devoted to taking notes on behavior of the animals in isolation. During these 68 periods, it was possible to get data on both Oka and Makoko so that each animal was studied an equal number of times. Every hour between 10:00 A.M. and 6:00 P.M. was covered. In addition to these systematic observations which started in July and lasted through the middle of August, 1948, each experimenter observed the gorillas several hundred times while passing through the Primate House to and from other areas in the Park. Any deviant behavior or peculiar activities were noted and added to the record.

## VI. Results and Discussion.

Two factors limit the analysis of the data. In the first place, quantitative analysis affords very little insight into the problem at hand. The purpose of this study was to obtain information which would serve as a starting point for further investigation of the gorillas at the Bronx Zoo, particularly as they become physiologically more mature and show active sex and social behavior. In the second place, it was thought desirable to point to both the similarities and differences between our gorillas and those at the San Diego Zoo described by Carpenter.

In this comparison, there are many difficulties and dangers arising from two sources. In the first place, the gorillas belong to different sub-groups, ours being lowland and Carpenter's mountain specimens. Other variables in this category include age and sex differences between the two sets of observed gorillas. In the second place, it is necessary to stress the differences in the environmental setting in which the San Diego and Bronx gorillas carried out their daily activity. At San Diego, the two male gorillas were housed in outside cages equipped with tree trunks for climbing and various devices which could be manipulated by the animals, for instance logs, swings, ropes, tires, etc. In addition, the experimenter could insert objects into the gorillas' surroundings and study the effect of such introductions. At the Bronx Zoo, the separation of the gorillas from the public was much more rigorous and the cages much more bare. In interpreting the comparative findings, the obvious individual and environmental differences must be kept in mind. However, despite these limitations, the comparison of the two groups should be of value, if only to emphasize the danger of generalizing from any set of observations.

With the restrictions specified above, the data in Table II represent the basic observations made upon the two gorillas at the Bronx Zoo. Where information comparable to that obtained by us was derivable from Carpenter's San Diego observations, it has been included in the Table. The discussion of the data in Table II will follow the general categories outlined above.

### *A. Posture and Locomotion.*

Posture and general locomotion seem fairly well established as invariant gorilla patterns. Both Carpenter's mountain and our lowland gorillas exhibited the same type and frequency of gross motor activity. Walking, running, standing and sitting were characteristically alike for Oka, Makoko and the San Diego pair. Differences were noted in the frequency of observed sleep and in swinging by the hands. Both of these differences may be the resultant of variable environmental and observational procedures. It was not feasible for us to observe night behavior, and swinging was made difficult for Oka and Makoko by the absence of a place suitable for that kind of activity. The complete absence of nest-building in the Bronx pair is also related to the lack of adequate materials. Both Carpenter and Yerkes report that it was a fairly common behavioral pattern in their subjects.

The observations on handedness in the Bronx gorillas are not comparable to other studies since this item was not listed by Carpenter. Oka was observed to make differential use of her hands on 313 occasions and Makoko 184 times. In both animals, the right hand was more frequently employed regardless of the nature of the activity. The frequency of use of this hand was 54% as compared with the report by Yerkes (6) who found that Congo used her right hand some 66% of the time. In Congo's case the left foot was preferred to the hand, whereas in our gorillas there was relatively little pedal manipulation.

### *B. Eating, Drinking and Elimination.*

In the presence of an abundance of food, Oka and Makoko both showed a form of behavior somewhat akin to the hoarding of rats and lower mammals. The gorillas would sweep the food into a heap with either the hands or feet. The heaped food was then examined, tossed around or eaten. This behavior is not mentioned in any other report on the gorilla and may well be the unique result of the absence of manipulatible material in the cages in the Bronx Zoo. Placing of the longer-stalked fruits and vegetables on the heads of the gorillas was a frequent aftermath of the in-gathering of the material.

An interesting aspect of the behavior of the isolated animals was a relatively infrequent passage of food from Oka to Makoko through the bars of the intercommunicating grill between the two cages. The initiation of this activity usually came from Oka and was noted particularly on the several occasions when Makoko had been deprived of his usual rations because of diarrhea or other health considerations. In such circumstances, Oka was observed forcing potatoes and cabbage through the double grill. Makoko did not seem to be particularly interested in the inserted foods. This behavior was seen on three occasions.

The drinking of water is a form of behavior common both to our animals and to those studied by Carpenter. According to Yerkes, Congo drank but little water. The manner of drinking in the Bronx animals was to bend over the fountain and suck the water into the mouth. Although there was no opportunity to study comparative satisfaction from milk and water, it is the opinion of the authors that the milk-egg liquid was preferred.

Regurgitation of the milk-egg mixture was almost invariable. Following the feeding the animals would typically squat on their haunches, lean forward, and regurgitate some if not all of the milk. The gorillas then would examine the liquid manually and eventually bend all the way and lick up the regurgitated material. The time interval after ingestion varied somewhat but was in the neighborhood of 45 seconds. Some chemical changes took place during the brief digestive stay for the milk was usually curdled. This pattern is seen not only in the gorillas at the Bronx Zoo but also in the chimpanzees. Whether or not this is a primate characteristic and analagous to the similar behavior of the pre-socialized human infant or whether it is unique to the subjects in captivity remains a matter for further research.

Voided fecal material was commonly handled both by Oka and Makoko and frequently was used to throw at the keepers, the observers or the public. Handling was casual and seemingly tactually motivated, for the feces were not examined nor used except for throwing. Since the keepers made heroic efforts to keep the cages clean, the opportunities for greater concentration on feces were limited. Carpenter makes no mention of this type of behavior. Urination was a casual affair and no localization of territory for this or for defecation was noted.

*C. Self-oriented Activity.*

Self-manipulation of parts of the body was a common form of activity in both Oka and Makoko. The parts of the body selected for handling or fingering were not consistent, with the exception of the lack of attention to or focus on the external genitalia. The major phase of activity during which handling was observed was while the gorillas were lying on their backs or stomachs, when parts of the body such as the lips, ears, eyebrows and nose would be held. The absence of genital manipulation may well be the result of the small size of the external genitalia of the gorilla, as described by Carpenter and Goss.

Manipulation of objects in the environment is a frequent finding wherever gorillas have been studied. Carpenter and Yerkes mention this behavior pattern and it was noticeable in the animals at the Bronx Zoo. The female, Oka, showed some tendency to manipulate and examine with greater frequency than her cage mate. In the absence of a variety of objects to examine, the frequency of occurrence of this activity is all the more remarkable.

The attitude of the gorillas toward the water fountain has already been described. An observable difference was noted in the behavior toward drinking water and that emanating from the pressure hoses used in cage cleaning. As indicated above, in the discussion of daily routine, water was used to separate the gorillas and to urge them toward the shift cages. The initial reaction to the stream from the hoses was retreat and excitement. However, once wet, the animals would face into the water and jump up and down. The keepers reported that the animals would on occasion approach more closely to the nozzle of the hose when thoroughly wet. No shaking of the body after the bath was seen during the periods of observation.

Self-grooming does not seem to be a dominant activity in the lives of either the San Diego or New York gorillas. To what extent the absence of this form of self-manipulation is a function of the cleanliness of the environment and the animal is not established by our observations but, as will be noted later, grooming as a pattern of behavior is markedly less present in the gorillas under study than in other primates at the Zoo.

*D. Inter-individual Behavior.*

The data in this section were obtained during those periods when the animals were together in the same cage. To the extent that the opportunity for such interaction was limited, the enhancement of activity during the periods of joint occupancy of the cage may be a function of the limitation of time during which the two animals could interact.

Both in Carpenter's study and in ours, the major forms of inter-individual activity were running, chasing and wrestling. These behavior patterns were well marked and almost stereotypical in appearance. Chasing was especially vigorous when the cage floor was wet and the gorillas spent much time sliding in a pronograde posture from one end of the cage to the other. Initiation of this activity was fairly evenly divided between Oka and Makoko. Wrestling, too, was not started consistently by either male or female. A dominance pattern was not apparent.

The sequence of individual motor acts in

TABLE II.

Comparative Behavior of Oka, Makoko and San Diego Gorillas.*

| Behavioral Classification | Frequency of Occurrence in San Diego | Oka | Makoko |
|---|---|---|---|
| A. *Posture and Locomotion* | | | |
| Walking, pronograde | +++ | +++ | +++ |
| Walking, upright | + | + | ++ |
| Running, pronograde | +++ | +++ | +++ |
| Running, upright | ND | + | + |
| Standing, pronograde | +++ | +++ | +++ |
| Standing, upright | + | + | + |
| Sitting | +++ | +++ | +++ |
| Climbing | ++ | + | + |
| Swinging by hands | ++ | + | + |
| Hanging | + | + | + |
| Sliding | +++ | ++ | ++ |
| Left-handedness | ND | 46% | 46% |
| Right-handedness | ND | 54% | 54% |
| Lying down | +++ | +++ | +++ |
| Sleeping | ++ | + | + |
| Nest Building | + | NP | NP |
| B. *Eating, Drinking and Elimination* | | | |
| Gathering food in heaps | ND | ++ | + |
| Sharing food with cage mate | O | + | + |
| Drinking water | +++ | ++ | +++ |
| Drinking milk | +++ | ++ | ++ |
| Regurgitation of milk | ND | ++ | ++ |
| Handling of feces | ND | + | + |
| Attention to urination | ND | + | + |
| C. *Self-oriented activity (Play?)* | | | |
| Self-manipulation (non-genital) | ++ | ++ | ++ |
| Manipulation of genitalia | O | O | O |
| Manipulation of objects | +++ | ++ | + |
| Manipulation of food (non-eating) | ND | ++ | ++ |
| Attitude toward stream of water | positive ++ | + | + |
| Self-grooming | ++ | + | + |
| D. *Inter-individual behavior* | | | |
| Chasing | +++ | +++ | +++ |
| Wrestling | +++ | +++ | +++ |
| Grooming | ++ | + | + |
| Inspection and manipulation of genitalia | O | O | + |
| Presenting | O | O | O |
| Mounting | O | O | O |
| Pelvic thrusts | O | O | + |
| Chest thumping | ++ | + | ++ |
| Vocalizing | ++ | ND | ND |
| Dominance | + | + | + |
| E. *Observer-oriented behavior* | | | |
| Throwing of feces | ND | + | ++ |
| Throwing of non-fecal material | ND | + | + |
| Attentional responses | positive ++ | negative ++ | negative ++ |
| Vocalization | ++ | ND | ND |

* Key to symbols:

O—Never observed or reported
+—Little in frequency or amount
++—Some or fairly frequent
+++—Great deal, very frequent
ND—No data reported
NP—Not possible in the environment

the wrestling behavior was free of patterning and seemed to consist of random grappling at the anatomical point nearest to the initiator of the behavior. When the actions of either animal seemed to approach the point at which roughness would ensue, the animal at the moment on the receiving end would detach itself and a period of resting would follow. Of all the behavior noted in this study, wrestling was the most dramatic and illustrative of the great strength of the gorillas. As a rule, there were few vocalizations during the bouts.

Social grooming, certainly, does not seem to be as predominant in the behavior of the gorillas as in the case of other representatives of the great apes or other primates. Carpenter likewise observed little of this sup-

posedly socially oriented activity. It is possible that in the four animals for which data are available, the age and sex differences were not sufficiently well established to facilitate the appearance of this type of social interaction. It may also be possible that there is a real species difference in such behavior.

Genital manipulation and exploration in the paired situation was not frequently observed. It was seen only three times in Oka and Makoko and was not reported for the San Diego pair. In the Bronx specimens, the initiator was always the male. This may be a reflection of the relatively greater maturity of Makoko. So, too, in our gorillas, mounting and pelvic thrusts as precursors of mating behavior were almost completely absent during the periods of observation in New York. Carpenter saw none of this at San Diego, but his animals were both males. The one instance of pelvic thrusts by Makoko occurred during a wrestling bout and was not repeated nor invited by Oka.

Chest-thumping was much more prevalent during the periods of paired activity than when the animals were in their own cages. The causal sequences leading up to the thumping could not be determined for Oka and Makoko although the observers were all of the opinion that the behavior was socially oriented and significant. Some writers have suggested that thumping of the chest is a sign of well-being and general euphoria. Yerkes states that the behavior is a sign of "impatience or other mild dissatisfaction." There was clear evidence of neither causal sequence in our observations. The range of situations during which the thumping was observed varied so widely that no specific factor can be assigned as the reason for its existence. The only statement that can be made from our data is that the male, Makoko, engaged in chest-thumping more frequently than did Oka and accompanied the beating with vocalizations more frequently than his companion.

In the absence of sound-recording devices, description of vocalization is difficult. Furthermore, the public space was somewhat soundshielded by the glass partition separating the animals from the observers. In our experience the occurrence of this activity was less than that mentioned by Carpenter.

*E. Observer-oriented Behavior.*

The types of audience-attentive behavior observed in the Bronx Zoo consisted mainly of the throwing of feces or food at the glass plate between the cage and the visitors. The same aggressive behavior was noted during an attempt to get photographs of the animals. Visitors invariably tried to attract attention from the gorillas by tapping on the glass partition and by yelling. The effect of such devices was negligible. This difference between our data and Carpenter's may well be the result of the more restrictive conditions of the gorillas' environment in the New York Zoo.

## VII. Summary.

This report describes the behavior of two pre-adolescent lowland gorillas in the New York Zoological Park during the summer of 1948. Oka, then an eight-year-old female, and Makoko, a ten-year-old male, were observed in their regular living cages when alone and when placed together.

A check-list was prepared and regular half-hour periods of observation were systematically made. Significant behavioral items were compared for the sessions when the animals were alone and when they were together. Comparisons were also made with the data collected by Carpenter from two male mountain gorillas in the San Diego Zoo.

The descriptive material obtained during the period of observation should serve as a base line from which to note variations arising from the maturation of the two gorillas in the years to come.

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## EXPLANATION OF THE PLATES.

### Plate I.

Fig. 1. Makoko, the male lowland gorilla in the New York Zoological Park. Estimated age, 11 years; weight, 408 pounds.

### Plate II.

Fig. 2. Oka, the female lowland gorilla in the New York Zoological Park, is still friendly and gentle with her keeper at the estimated age of 9 years. Her weight is 282 pounds.

Fig. 3. Oka playing with her keeper.

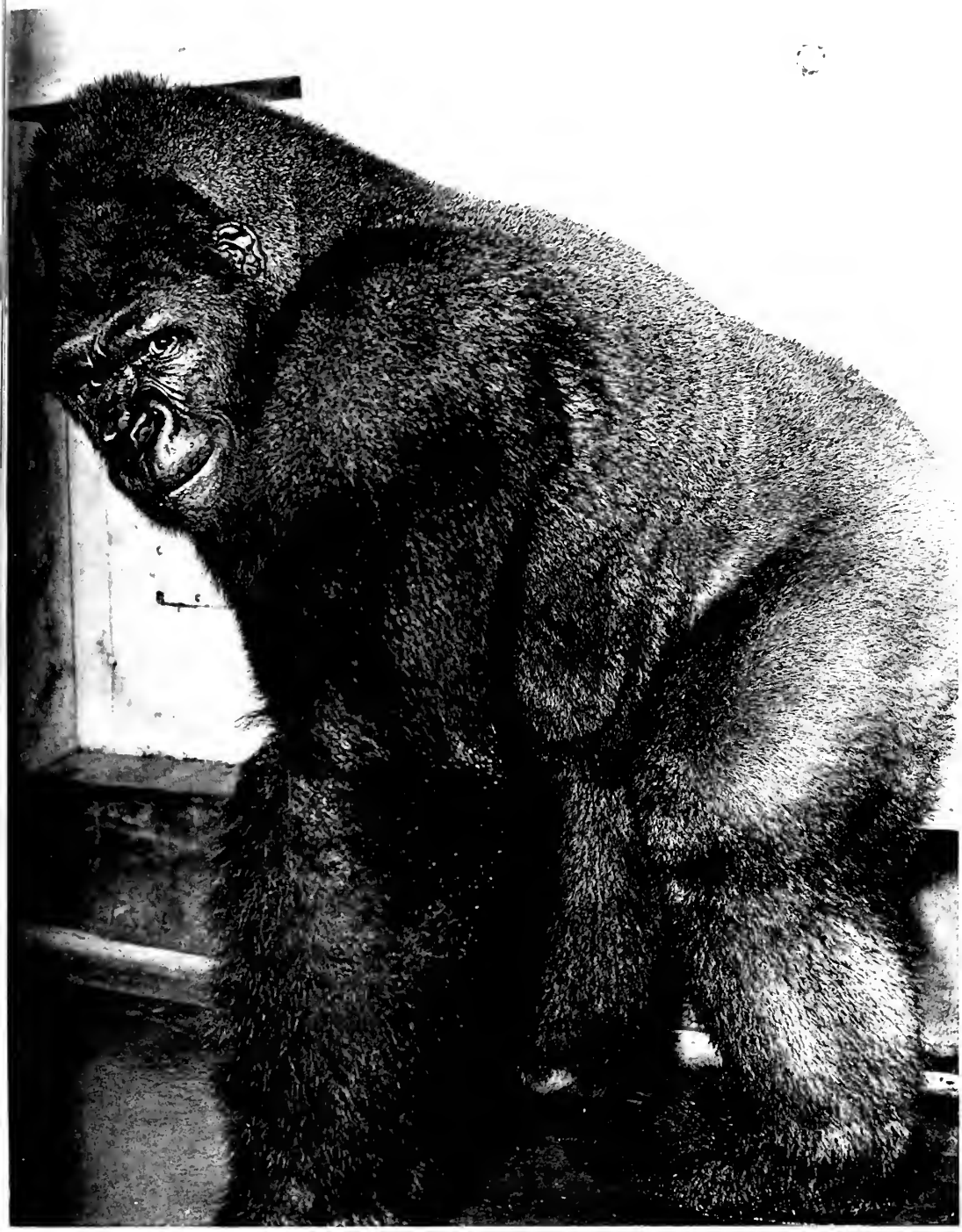

FIG. 1.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA, GORILLA GORILLA GORILLA (SAVAGE & WYMAN).

FIG. 2.

FIG. 3.

THE BEHAVIOR OF TWO CAPTIVE SPECIMENS OF THE LOWLAND GORILLA, GORILLA GORILLA GORILLA (SAVAGE & WYMAN).

# 14.

## Migration of Papilionidae at Rancho Grande, North-central Venezuela.[1]

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(Plate I; Text-figure 1).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948, under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows; Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. The migration flyway of Portachuelo Pass, which is also the water-shed between the Caribbean and Lake Valencia, is 200 meters from Rancho Grande. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both wet and dry seasons, was 92.4%; the average temperature during the same period was 18° C; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

For an account of Portachuelo Pass, together with a general introduction to the groups of migrating insects and migrating factors see "Insect Migration at Rancho Grande," by William Beebe, *Zoologica*, 1949, Vol. 34, No. 12, pp. 107-110.

In Volume 26 of *Novitates Zoologicae*, W. J. Kaye has a paper entitled "A Geographical Table to show the Distribution of the American Papilios." Under the heading "Venezuela, North," (pp. 352-355), the author lists thirty-one species. In a letter Dr. Rene Lichy of Caracas sends me a list of thirty-one species of this family which he has collected in northern Venezuela. A continuation of this coincidence is that each list contains seven species not found in the other list.

Both lists contain all the species which we took migrating through Portachuelo Pass, with the single exception of *crassus* which Lichy does not mention.

In the limited width of twenty meters of Portachuelo Pass, and allowing a height of net reach of a maximum of five meters, we captured seventeen species of *Papilio*. This area may be considered, not unrealistically nor unconservatively, as, at the most, a millionth of the extent of north Venezuela. Yet within this relatively microscopic bit of Andean air, we secured almost half the papilios so far recorded from the entire northern part of the country. Thus, in the consideration of this family of butterflies, we are made to realize the wide-spread, impelling, migrational force affecting this group of insect life.

So much of this migration—its causes and extent—is at present unknown, that every verifiable fact is of value. Reviewing the known distribution of the seventeen species of *Papilio* migrants, we find that most of them extend from Mexico to Paraguay, south Brazil or Argentina. The distribution of the subspecies, however, presents a very different picture, and a very significant one in its over-all pattern. In twelve out of the seventeen, the subspecific range is confined to Colombia and Venezuela, with a few extensions to adjacent territory. Thus we may expect to find the northern point of origin of the movement of these forms a relatively short distance away.

The twelve subspecies of *Papilio* with limited distribution are as follows:

*anchises osyris*
*anchisiades anchisiades*
*agesilaus agesilaus*
*arcas arcas*
*cleotas coroebus*
*erithalion zeuxis*
*lycophron hippomedon*
*paeon thrason*
*polyxenes americus*
*protesilaus archesilaus*
*sesostris tarquinius*
*torquatus orchamus*

1 Contribution No. 852, Department of Tropical Research, New York Zoological Society.

The remaining five forms of *Papilio* with wider distribution are:

*belus varus*
*crassus*
*phaon*
*polydamus polydamus*
*thoas neacles*

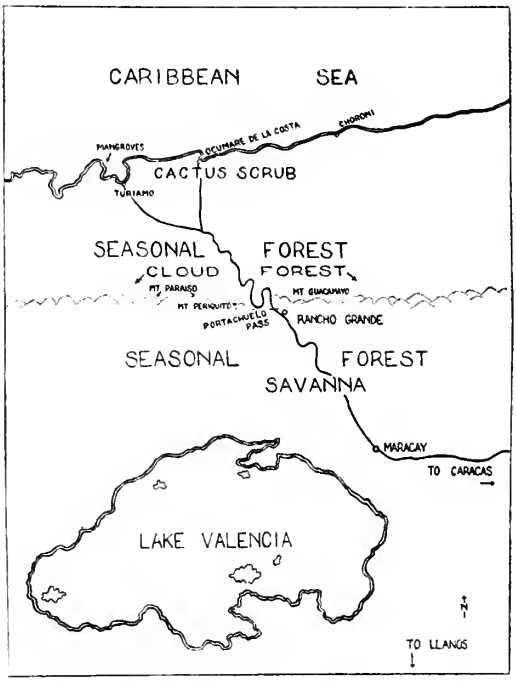
Let us take as an example *Papilio agesilaus agesilaus* or, as I called it before identification, Small Zebra Swallowtail. I recorded seven individuals captured and fifty-eight seen with certainty. Added to this number were the many papilios glimpsed too briefly, flying too high or too fast to be recognized as to species, and also those which must have passed during the hours of our absence from the pass. It was heartbreaking to realize what a minute fraction we could honestly record by sight identification, yet there is no other way, at present known, to glean definite, general knowledge of this phase of the lives of these splendid insects. Without exception, all sight-named species were subsequently confirmed or discarded by comparison with captured, definitely classified specimens.

In this as in some other species, the small number of records from the year 1946 and their entire absence from 1945 by no means indicates the absence of the species on migration, but only reflects our non-recognition of the importance of the Portachuelo Pass migration during the early years, and consequent slight attention paid to this phenomenon. An ultimate summary of the relatively few, disconnected observations made during 1945 and 1946 reveals a general movement on a scale equal in magnitude and as all-embracing of insect orders as we recorded during 1948.

The mere recording of the capture of seventeen species of *Papilio* on migration is a worth-while fact, and when more and more individuals are taken on suceeding days and weeks the phenomenon is enhanced in interest. In few or in large numbers the insects continue to fly past, slowly or circling or alighting out of reach. As in the case of many other organisms, the time has come when sight records must be used to supplement specimens in net, envelope and cabinet. Ornithologists in general and British entomologists in particular have gone far in sight identifications, while at the same time maintaining as perfect accuracy as possible with man's fallible eyesight and only too human brain.

At the end of our many months of collecting and observation at the pass, I found, in my Journal, a significant assemblage of shorthand names of papilios. They were, of course, essentially personal, stimulated by mental comparisons with swallowtails familiar to me elsewhere, or in the case of strange tropical forms, by outstanding wing shapes, size, patterns and colors.

Lepidopterists recognize three "natural groups" into which papilios may be divided.




TEXT-FIG. 1. Map showing location of Rancho Grande, Portachuelo Pass and surrounding territory.

These are based on various factors such as larvae, pupae, microscopical imaginal distinctions and/or food-plants. Our migrant species fit into these three groups as follows: ARISTOLOCHIA: *sesostris, erithalion, anchises, arcas, polydamus, belus* and *crassus*. FLUTED: *polyxenes, thoas, paeon, lycophron, anchisiades, torquatus* and *cleotas*. KITE: *phaon, agesilaus* and *protesilaus*.

Consideration of this arrangement shows no logical, technical or scientific agreement. This is only to be expected in sight identification, which can take no account of sexual relationships, or parallelisms, or the superficial resemblance brought about by mimicry.

After final identification of the seventeen species of *Papilio* migrants, I arranged mounted specimens of all in a large insect drawer, placed this upright on a chair in good light and studied them from a distance of ten meters. From this distance I made the following key:

A—WHITE AND BLACK
- a—Small: *agesilaus agesilaus*
- b—Large: *protesilaus archesilaus*

B—YELLOW AND BLACK
- a—Yellow-banded
  - Broad-band-plus-spot, small: *torquatus, orchamus*, male
  - Broad-band, medium: *lycophron hippomedon*, male
  - Narrow-band: *paeon thrason thoas neacles*

b—Yellow-spotted
Small: *polyxenes americus*
Medium: *polydamus polydamus*
Large: *cleotas coroebus*

C—Red and Black (Hindwing)
a—Cream-spot-forewing
*sesostris tarquinius*, female
*erithalion zeuxis*, female
*anchises osyris*, female
*arcas arcas*, female
*torquatus orchamus*, female
b—Green-spot-forewing
*erithalion zeuxis*, male
*anchises osyris*, male
*arcas arcas*, male
c—Black-forewing
*anchisiades anchisiades*

D—Green and Black
a—Green-forewing
*sesostris tarquinius*, male
b—Green-hindwing
*phaon*

E—Black (Dominantly)
*belus varus*
*crassus*
*lycophron hippomedon*, female

I compared this key with the names made up on the spot in the field, and found a gratifying agreement in species recognition. The differences were chiefly substitution for patterns and colors of the names of northern species suggesting resemblances, species with which I had long been familiar in the eastern United States. For example, *agesilaus agesilaus* was "small ajax or zebra," *polyxenes americus* was "small asterias," and *thoas neacles* was "cresphontes-like," etc.

I cite all this as in no way directly possible or in the same detail applicable for use by another observer, but merely to show a framework upon which can successfully be erected an observer's sight key. Further comments, in greater or less detail, will be found under the treatment of many of the species.

My special thanks go to Mr. Henry Fleming, entomologist of our Department of Tropical Research, for many direct observations and for frequent corroboration of my own. In addition I am beholden to him for looking up distribution data and for painstaking identification of all the species.

**Papilio anchises osyris** Felder.

Species Range: Colombia to Brazil, Bolivia and Paraguay.

Subspecies Range: Venezuela.

Field Characters: Both male and female indistinguishable in the field from *erithalion zeuxis*. Therefore all specimens observed and not taken are combined under the two species. Compared with *arcas arcas* the male lacks bright green forewing spot, and the female has a decidedly larger, 4-celled forewing cream spot.

Number and Sex: Both sexes taken; eight males, five females.

Date: April 13 to July 29.

Condition: All taken were fresh.

Record of Captures: 1945—July 15 (male), 18 (female). 1946—April 13 (male, km. 20). 1948—April 29 (male); May 1 (female), 31 (female); June 6 (male and female); July 17 (male, km. 30), 23 (male, km. 15), 29 (female at Pass, 2 males, km. 35).

Combined Sight Records: *anchises* and *erithalion*: (Total 62). 1946—May 27 (4 females); June 29 (2 females). 1948—May 26 (4 females); June 4 (11 females passed in 10 minutes), 15 (4 females resting on shrubs), 22 (5 seen); July 2 (12 females), 9 (14 males, 3 females), 29 (3 females).

**Papilio anchisiades anchisiades** Esper.

Field Name: Red-spot Black.

Species Range: Mexico to southern Brazil.

Subspecies Range: Colombia to Bolivia and Para (Brazil).

Field Characters: Black with red on hindwing. Closest in field appearance to wholly black *lycophron hippomedon*.

Number: 2 specimens taken, a male and a female.

Notes: This black-forewing-red-hindwing papilio came through the Pass with what were taken and identified as female *arcas arcas* and *anchises osyris*, all captured together.

Record of Captures: A male in frightfully worn condition collected on April 13, 1945, No. 45456. A second individual, a female, taken at the Pass May 1, 1948, No. 48474.

**Papilio agesilaus agesilaus** Guerin.

Field Name: Small Black-and-white Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Magdalena Valley, Colombia, to northern Venezuela.

Field Characters: Unmistakable resemblance to our northern ajax or zebra. The only optically related species is *protesilaus archesilaus*, but the present species is much smaller (forewing 43 mm. as compared with 53 mm.). The difference easily recognizable when either species is close at hand or near other butterflies.

Number: Total recorded 58. Seven taken (48543, 48731, 481344, 481494).

Sex: Both sexes taken.

Date: From April 29 to July 26.

Frequency: Recorded on seventeen days. Moderately but markedly gregarious. Two-thirds of *agesilaus* were recorded in groups of 4 to 8, while one-third appeared singly or in twos.

Flight: Except when alarmed or fighting against a strong head wind, the flight was unhurried and wavering, always steadily south.

Condition: With one exception all that I saw hovering or resting at the Pass were in

good condition, with both long slender tails visible to the naked eye or through three-power binoculars. No. 481344, taken July 26, 1948, at kilometer 16, was badly mutilated, with one tail missing. Dissection revealed that this male had already mated.

Record: 1946—May 26 (2 seen), 27 (2 at Pass, 3 at km. 20), 30 (6 singly). 1948—April 29 (2); May 14 (1 taken), 21 (4 seen, 1 taken), 23 (1 taken), 24 (4), 26 (4), 31 (8); June 6 (1), 17 (2 taken), 19 (2); July 13 (4), 16 (2), 23 (1 taken km. 16), 24 (6), 26 (1 at Pass, 1 at km. 16).

**Papilio arcas arcas** Cramer.

Field Name: Green-spot (male). Two-celled-cream-spot (female).

Species Range: Mexico to Colombia, Venezuela and the Guianas.

Subspecies Range: Venezuela and the Guianas.

Field Characters: Closest to *anchises* and *erithalion*, from which it differs in the bright green forewing spot in the male, and the smaller, two-cell forewing spot in the female. It is also close to the exceedingly rare *torquatus orchamus*. From the male *sesostris tarquinius* this species differs in the red on the hindwing.

Number: Total recorded 277. Twenty-one taken.

Sex: Both sexes taken. In 1946 only females were seen or taken. In 1948 females were dominant from May 1 to June 17, and males from July 6 to July 22.

Date: May 1 to July 22.

Frequency: Recorded on 20 days: 1 (15 times), 2 (4 times), 4 (once), 6 (twice), 7, 13, 14, 16, 18, 29 and 85. Decidedly gregarious, occurring singly and in twos nineteen times, comprising one-fourteenth of the total number passing in larger numbers—from 4 to 85. As mentioned above, the sexes showed a decided segregation. The flocks were usually compact waves.

Flight: Rather low and fluttering.

Condition: Most of *arcas* observed were in fresh condition, decidedly unworn.

Extent of Migration: On four separate days specimens of this species were taken both at the Pass and at kilometer 20, well to the south, and at kilometer 35, half way to the coast to the north.

Record: 1945—July 3 (3 taken), 16 (2 seen, 1 taken, Limon). 1946—May 28 (27 seen, 2 taken), 29 (7 at Pass, 6 at km. 20), June 4 (female), 22 (female); September 7 (84 in half an hour, 1 taken). 1948—May 1 (female), 4 (6 females), 5 (male), 28 (female) 29 (female); June 6 (2 males, flock of 18 females), 17 (16 females flying low), 22 (male and female), 28 (28 females); July 6 (2 males), 9 (male caught and eaten by bat falcon, 21 males seen), 14 (7 males), 15 (11 males, 3 taken), 16 (13 seen, four fighting in midair), 19 (4 males, 1 taken km. 15), 22 (2 males, 1 taken km. 35).

**Papilio belus varus** Kollar.

Species Range: Mexico to Bolivia and Para (Brazil).

Subspecies Range: Guatemala to northern Venezuela and Ecuador.

Dichromatic Female, form *latinus* Felder.

Field Name: Greenish-hindwing-band Black.

Field Characters: Black, with a curved band of large, yellow-green spots on hind wing.

Number: Total recorded 19. Eight taken.

Sex: Females only taken.

Date: May 29 to August 4.

Frequency: Taken singly. Five once seen together.

Condition: Fresh.

Record: 1946—July 7 (1 seen km. 20). 1948—May 29 (1 seen); July 4 (4 seen at 8:30 A.M.), 14 (1 taken), 16 (3 taken), 21 (2 taken, 3 seen), 26 (1 taken, 2 seen km. 16); August 4 (1 taken).

Dichromatic Female, form *varus* Kollar.

Field Name: Cream-spot-forewing Black.

Field Characters: Irregular splash of yellow in forewing; hindwing blue-black.

Number: Total recorded 18. Three taken.

Sex: Females only taken.

Date: May 30 to July 26.

Frequency: On two occasions, five were seen together.

Condition: Fresh.

Record: 1948—April 29 (1 taken); May 30 (5 seen); July 8 (3 seen), 9 (2 seen alighted, 2 taken, 5 seen km. 31).

**Papilio cleotas coroebus** Felder, form *dione* Rothschild and Jordan.

Field Name: Large Asterias Swallowtail.

Species Range: Costa Rica to Brazil.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Rather like a very large Asterias, or *polyxenes americus*, with forewing 67 mm. as compared with 40 mm. A very distinct species.

Number: Total recorded 19. One taken.

Sex: The single specimen taken was a female.

Date: May 26 to July 17.

Record: 1948—May 10 (4 seen), 26 (2 seen); June 6 (female taken, 2 others flying in company with three of the small *polyxenes americus*); July 10 (2 at Pass, 2 at km.15), 17 (3 at Pass, 3 at km. 30).

**Papilio crassus** Cramer, male form *lepidus* Felder.

Field Name: Black Philenor.

Species Range: Costa Rica south to Brazil.

Field Characters: Wholly black except for concealed bluish-white anterior border of hindwing.

Number: Total seen 23. One taken.

Record: A single male specimen of the form *lepidus* taken on July 21, 1948, No. 481538. Twenty more, distinctly seen, passed

at the same time, all out of reach. On the following day, July 22, two more of these black papilios were seen. No other record.

**Papilio erithalion zeuxis** Lucas.

Species Range: Costa Rica to Colombia and northern Venezuela.

Subspecies Range: North Venezuela and Colombia.

Field Characters: Both sexes indistinguishable from *anchises osyris*. Differs from *arcas arcas* in male lacking forewing green spot, and female with larger, 4-celled forewing cream spot.

Number: Total number taken 14.

Sex: Both sexes taken.

Date: June 29 to July 24.

Condition: All freshly emerged.

Record of Captures: 1945—July 3 (female taken, Limon). 1946—June 29 (female, km. 20); July 7, 8 and 10 (Each day 1 female taken, km. 20). 1948—July 9 (3 males, km. 31), 14 (male), 15 (male), 17 (2 females), 23 (female, km. 15), 24 (female).

For joint sight identification records with *anchises osyris*, see under latter species.

**Papilio lycophron hippomedon** Felder.

Field Name: Male, Broad-band Medium Turnus. Female, Black Troilus-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male can be confused only with the very rare, smaller, yellow-spot *torquatus orchamus;* female recalling a melanistic *troilus* or *phaon* with black hindwings.

Number: Total recorded 20. Eight taken.

Sex: Both sexes taken.

Date: May 10 to July 20.

Record: 1946—May 27 (2 at Pass, 2 km. 20, all males). 1948—May 10 (3 males seen), 21 (female taken), 23 (male taken), 24 (male taken), June 6 (2 females taken), 17 (2 males taken), 29 (4 males seen); July 10 (male seen), 20 (male taken).

**Papilio paeon thrason** Felder.

Field Name: Rare Cresphontes-like Swallowtail.

Species Range: Mexico south to Argentina and Uruguay.

Subspecies Range: North Colombia and Venezuela.

Field Characters: Indistinguishable in the field from *thoas neacles*, but as only a single specimen of *paeon thrason* was taken, compared with more than one hundred of *thoas*, I am assuming that all Cresphontes-like papilios observed were of the more abundant species.

Record of Capture: A single male taken on May 23, 1948, No. 481539, in extremely torn and worn condition. It was captured at the Pass at 12:30 P.M., the day being warm and sunny with a Force 4 wind from the south.

**Papilio phaon** Boisduval, aberration *metaphaon* Butler.

Field Name: Philenor-like Swallowtail.

Species Range: Mexico to Ecuador and Venezuela.

Field Characters: This is the only black papilio with green on the hind wings.

Number: Total recorded 254. Seven taken.

Sex: Both sexes taken.

Date: April 13 to July 21.

Record: 1945—May 24 (1 taken). 1946—(September 9, numbers of these black papilios with large green spot on the hind wings were flying too high to catch. Several alighted and allowed detailed study with Number three glasses. Counted 228 and missed many more.) 1948—April 13 (male taken km. 20), 16 (male taken), 27 (male taken, km. 20), 29 (female taken at Pass); July 21 (2 taken, 19 seen).

**Papilio polydamus polydamus** Linnaeus.

Field Name: Medium Asterias Swallowtail.

Species Range: South Atlantic states, West Indies and south to Argentina.

Subspecies Range: Georgia south to Buenos Aires.

Field Characters: Differs to the eye from *polyxenes americus* in the field by the single instead of double line of yellow spots across all wings. Another distinction is the larger size.

Number: Total recorded 177. Nine taken.

Sex: Both sexes taken.

Date: May 15 to July 26.

Frequency: Decidedly gregarious. One-eighth passed singly or in a scattering up to five individuals. Seven-eighths were observed in flocks of ten to forty-eight.

Record: 1946—May 27 (2 seen). 1948—May 15 (5 seen), 29 (female taken); June 6 (female taken), 22 (11), 30 (female taken, 48 passing, 2 seen at km. 21). July 9 (female taken), 10 (2 males taken, 16 seen. 2 taken km. 31), 11 (14 flurry, 1 single), 14 (1 taken, 23 seen), 17 (10 seen km. 30), 18 (3), 19 (3), 22 (3 km. 35), 26 (27 seen).

**Papilio polyxenes americus** Kollar, form *melasina* Rothschild and Jordan.

Field Name: Small Asterias Swallowtail.

Species Range: Canada south to Cuba and Peru.

Subspecies Range: Colombia, Venezuela and northern Peru.

Field Characters: Under a new name this proved to be the same species as our northern Asterias. The only other resembling migrant butterfly was the markedly larger *polydamus polydamus*.

Number: Total observed 34. Although observed on ten occasions during two seasons, only three specimens were taken.

Date: March 25 to July 20.

Frequency: 1, 1, 1, 2, 2, 2, 3, 3, 3, 6, 6.

Note: Three perfect specimens on June 5, after rain, clung to the extreme ends of large leaves. The wings were flat and expanded, with the fore edge straight across so that the transverse band and spots were continuous.

Record: 1946—March 25 (1 taken, km. 21); April 19 (1 taken, km. 21); May 28 (2 seen at Pass). 1948—April 29 (3 seen); May 4 (6 flying together), 28 (2 seen); June 5 (3 seen), 6 (3 seen); July 19 (6 seen), 20 (1 taken at Pass), 22 (6 seen at km. 35).

***Papilio protesilaus archesilaus*** Felder.

Field Name: Large Zebra Swallowtail.

Species Range: Mexico to Paraguay.

Subspecies Range: Colombia, northern Venezuela and western Ecuador.

Field Characters: Larger than (forewing 53 mm. as compared with 43 mm.) but in general similar to *agesilaus*. Size difference quite apparent when near, but not when flying high, away from other known butterflies. At least fifteen individuals were not counted because of uncertain sight identification.

Number: Total recorded 42. Three taken (48543).

Sex: Males only were taken. The female seems to be quite unknown.

Date: Recorded on migration from April 29 to July 19.

Frequency: The relative gregariousness corresponds to that in *agesilaus*. More than five-sixths were in 4 to 12 groups, and six only seen as solitary or dual migrants.

Condition: All observed in detail appeared fresh and perfect.

Additional Notes: The flurry of 12 large zebras on May 30, were in a compact body, and at a time when neblina and rain, while light, were continuous enough to discourage all other migrants. Yet these great swallowtails flew steadily at a height of about 12 feet, up to and through the Pass and down into the fog on the south slope.

The actions of six which passed on May 26 were typical. All flew slowly and with slightly wavering flight at 10 feet, until I swooped futilely at them with the net when all swerved sharply out and down, two penetrating the underbrush and working their way separately through the Pass before rising into the free air again. Three were followed with the glasses far down the south slope.

Record: 1946—May 27 (1 seen, 1 at km. 20), 29 (4 seen, 1 taken). 1948—April 29 (4); May 1 (3), 4 (1 taken), 10 (1), 21 (5 seen, 1 taken), 26 (6), 30 (12); July 19 (1 at Pass, 1 at km. 15).

***Papilio sesostris tarquinius*** Boisduval.

Field Name: Male, Green-spot Black.

Species Range: Mexico to Bolivia and central Brazil.

Subspecies Range: Panama, Ecuador, northern Venezuela.

Field Characters: Male to be confused only with male *arcas arcas*, but wholly lacks the hindwing red.

Number: Total recorded 39. Three taken.

Sex: Males only taken.

Date: April 30 to July 20.

Frequency: 1, 4, 5, 6, 23.

Condition: All freshly emerged.

Record: 1948—April 30 (1 taken); June 10 (4 seen), 17 (6 seen), 22 (22 seen, 1 taken); July 20 (4 seen, 1 taken).

***Papilio thoas neacles*** Rothschild and Jordan.

Field Name: Common Cresphontes-like Swallowtail.

Species Range: Texas to Buenos Aires.

Subspecies Range: Nicaragua to Ecuador, Venezuela, Trinidad and the lower Orinoco.

Field Characters: Cresphontes-like. Unidentifiable, even at close range, from *paeon thrason*, but only a single specimen of the latter was taken in two years of collecting.

Number: Total recorded 105. Nine taken.

Sex: Both sexes taken.

Date: May 4 to September 8.

Frequency: Usually seen passing in small groups, five to eight, maximum sixteen. Strong flyers, difficult to capture, but occasionally alighting, affording opportunity for a good look.

Record: 1946—May 4 (male taken, km. 20), 27 (16 seen); July 7 (female taken, km. 20); September 8 (3 seen). 1948—April 29 (3 seen), 30 (3, km. 26, headed for Pass); May 1 (4), 10 (2), 11 (2), 15 (4 seen, 1 taken), 23 (8 seen, male taken), 26 (6), 31 (1 seen); June 6 (3 taken, male, 2 females. Eggs protruding from females), 10 (5), 18 (8), 22 (6), 29 (4), 30 (5); July 2 (5 seen), 9 (2 at Pass, 6 km. 31), 13 (male taken), 19 (3 seen, 1 taken km. 18).

***Papilio torquatus orchamus*** Boisduval.

Field Name: Male, Small Yellow-Band-and-Spot. Female, mimic of *arcas*.

Species Range: Mexico to Bolivia, Brazil and Paraguay.

Subspecies Range: Colombia and northern Venezuela.

Field Characters: Male somewhat similar to but smaller than male *lycophron hippomedon;* female very close to female of *arcas arcas*. The large, separate, anterior yellow spot on forewing of the male distinguishes it from the solid band of *lycophron*.

Number: Two males were seen, and two females taken.

Sex: Both sexes seen, female only taken.

Dates: May 1 to July 2.

Record: On May 1, 1948, I watched two new papilios fighting in the Pass. One flew down and alighted just out of reach, and the other soon followed. I made a detailed description of them, recording them as yellow-

banded-with-spot, tailless papilio. Not until our return north were we able to identify the insects by comparison with a male *torquatus* taken at Caripito.

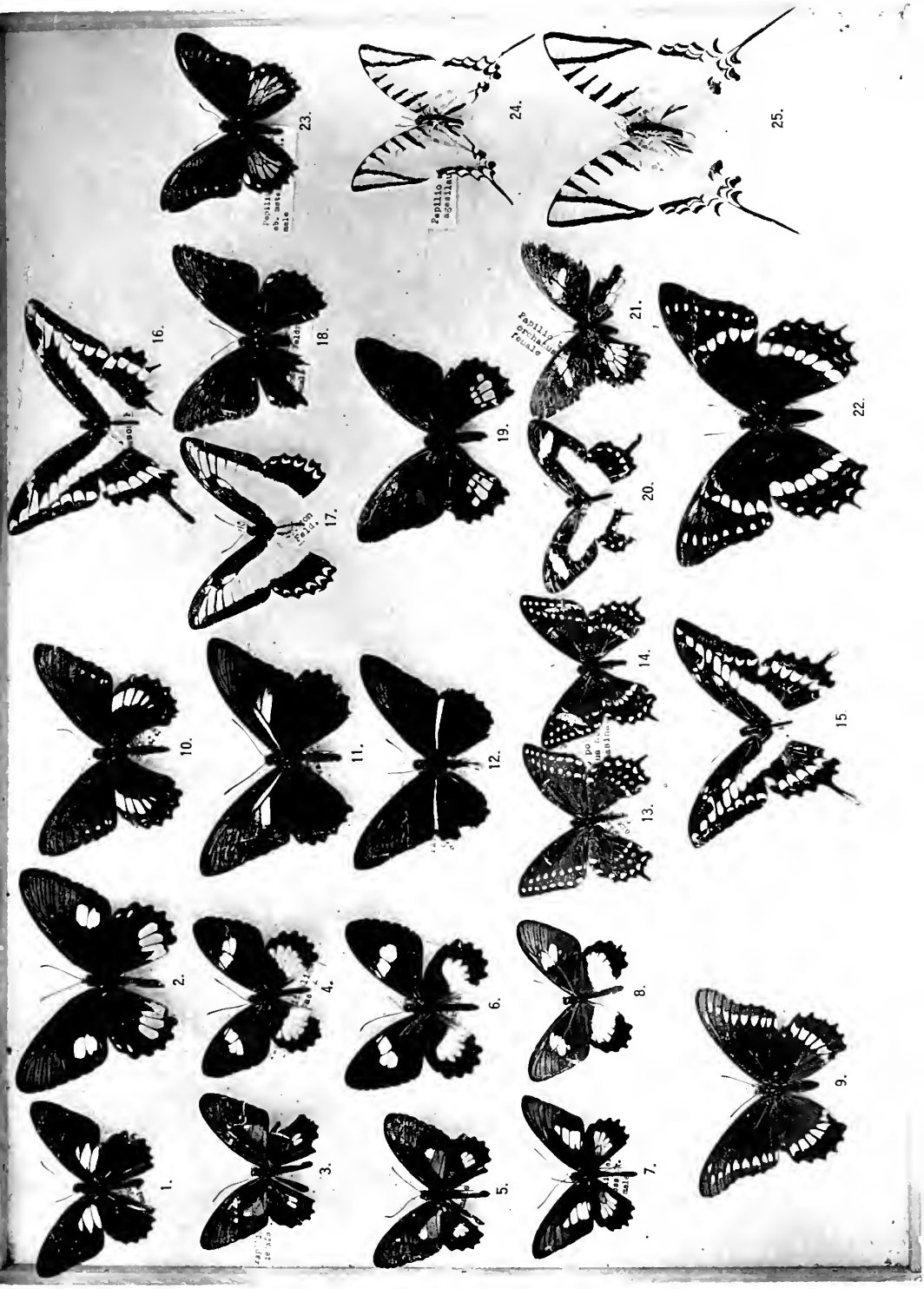
On May 26 and again on July 2, 1948, a female was taken. These were badly rubbed and torn, whereas the males I saw were freshly emerged.

## EXPLANATION OF THE PLATE.

### PLATE I.

Seventeen species of butterflies of the genus *Papilio* taken as migrants at Portachuelo Pass, Rancho Grande, north-central Venezuela.

Fig. 1. *sesostris tarquinius* (male).
Fig. 2. *sesostris tarquinius* (female)
Fig. 3. *erithalion zeuxis* (male).
Fig. 4. *erithalion zeuxis* (female).
Fig. 5. *anchises osyris* (male).
Fig. 6. *anchises osyris* (female).
Fig. 7. *arcas arcas* (male).
Fig. 8. *arcas arcas* (female).
Fig. 9. *polydamus polydamus.*
Fig. 10. *belus varus* form *latinus.*
Fig. 11. *belus varus* form *varus.*
Fig. 12. *crassus* form *lepidus.*
Fig. 13. *polyxenes americus* form *melasina* (male).
Fig. 14. *polyxenes americus* form *melasina* (female).
Fig. 15. *thoas neacles.*
Fig. 16. *paeon thrason.*
Fig. 17. *lycophron hippomedon* (male).
Fig. 18. *lycophron hippomedon* (female).
Fig. 19. *anchisiades anchisiades.*
Fig. 20. *torquatus orchamus* (male).
Fig. 21. *torquatus orchamus* (female).
Fig. 22. *cleotas coroebus* form *dione.*
Fig. 23. *phaon* aberration *metaphaon.*
Fig. 24. *agesilaus agesilaus.*
Fig. 25. *protesilaus archesilaus.*




MIGRATION OF PAPILIONIDAE AT RANCHO GRANDE,
NORTH-CENTRAL VENEZUELA.

# 15.

## Notes on *Ergasilus* Parasites from the New Brunswick, New Jersey, Area, with a Check List of All Species and Hosts East of the Mississippi River.

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### INTRODUCTION.

The members of the genus *Ergasilus* represent the most undifferentiated of all the copepod parasites and clearly show a possible line of evolution from the free-living forms to the very specialized parasites that are to be found in other families and genera. Even in the genus itself one finds the transition taking place, and *E. chautauquaënsis* (which has never been found as a parasite) to *E. elegans*, which is parasitic only after the eggs begin to develop, and on to the other forms where the females are parasitic after they have become sexually mature.

The main characteristics of the genus are its cyclops-like appearance; 2nd pair of antennae enlarged and prehensile, 1st antennae six-jointed; first thoracic segment and head fused to form a large carapace; five pairs of swimming legs; the first four biramose, the fifth pair very degenerate and uniramose. Egg sacs are similar to those in *Cyclops*. The genus is typically fresh-water, though some ergasilids are to be found in brackish and marine waters. The type species of the genus is a very common European species, *E. sieboldi*, established by Nordmann in 1832.

These parasites are generally found clinging to the gill filaments, but one species, *E. megaceros*, has been found in the nasal fossae of the Fulton cat, *Ictalurus anguilla*, and another, *E. elongatus*, has been found attached to the bony gill rakers of the spoonbill cat, *Polyodon spathula*. At the present time they have been found to infest all of the major groups of fresh-water fishes and it is likely that no species of fresh-water fish is entirely free from the possibility of becoming a host. As far as is known, fishes are the only hosts on which this genus has ever been found. (See Mueller, 1936; Tidd & Bangham, 1945; Wilson, 1911, 1916, 1925, 1932; Wright, 1844.)

The males of *Ergasilus* are free-swimming throughout their lives. They are small and easily overlooked in plankton samples and consequently few of them have ever been described. The chief distinguishing characteristics in the males are the powerful maxillipeds, which are lacking in the females, and the small, weak second antennae.

The females are free-swimming during their early developmental stages and only attach themselves after mating. It is generally concluded (Wilson, 1911) that mating takes place only once while the female is still free-swimming. The sperms are stored in the semen receptacle and fertilize the eggs as they pass out into the ovi-sacs.

The breeding season apparently extends throughout the summer months. The length will vary from season to season, or from one region to another, depending on favorable water temperatures. In this area females were observed with fully extended egg strings on March 31. In the laboratory the incubation period was found to be around eight weeks, which is about the period of time observed by Wilson ("eight to nine weeks"). Henderson (1926) in her paper on *E. lucionercarium* from Canada, stated that it is likely that the females carry their egg strings throughout the winter. This is not the case in Westons Mills Reservoir, but it may be that in Canada, where the summer season is considerably shorter, the last batch of eggs does not get the chance to develop before cold water temperatures come and consequently must be carried over until the warmer temperatures of spring. In New Brunswick the breeding season is over by the middle of November.

### OBSERVATION ON EPIDEMIC OF *Ergasilus* ON FISHES IN THE WESTONS MILLS RESERVOIR, NEW BRUNSWICK, N. J.

During the latter part of November, 1947, fishermen began to notice large numbers of fish dying in Westons Mills, a reservoir from which New Brunswick obtains its water supply. Local residents estimated that the fish were dying by the "thousands," and indeed the number of dying fish was so great

[1] The author wishes to express his appreciation to Mr. Herbert Groat, who first called attention to the epidemic; Dr. R. F. Nigrelli for assistance in making this paper ready for publication; and to Herbert Treuting and others who gave assistance when it was needed.

as to attract large flocks of sea gulls from the nearby Raritan River. The fish affected were apparently only two species, calico bass, *Pomoxis sparoides*, and bluegill, *Lepomis macrochirus*.

Some of these fish were brought to the Rutgers University Zoological Laboratory where they were examined for possible parasitic infestations. No intestinal parasites were found in excessive numbers nor did there appear to be any injury of body tissues, either external or internal. The gills appeared to be covered with an unusually heavy coating of mucus and microscopic examination revealed great numbers of copepod parasites of the genus *Ergasilus*. The blue color of these organisms, the three knobs on the inner edge of the second antennae towards the distal end, and the fact that they were all found in between the gill filaments seemed to indicate conclusively that these were of the species *caeruleus*. The hairs and spines on the appendages, along with other general morphological characteristics, were not quite in accord with Wilson's *caeruleus*, but there seemed to be a considerable amount of variation in this genus, depending on geographic location (Mueller, 1936). Wilson (1911) considers *caeruleus* a parasite of the vegetative Centrarchidae, and gives the explanation that the copepods on these fishes must locate themselves between the gill filaments to escape the discomfort and irritation to their gills from bits of vegetation.

A number of trips were made to the reservoir to collect fish during this period. Oxygen determinations were made at all depths and at no time was the $O_2$ concentration less than 10 ppm. Most of the fish were alive when captured. They could easily be spotted as they swam feebly on their sides on the surface of the pond. It was possible to come up alongside these fish in a boat and pick them up by hand. Occasionally a fish would sound on approach, but only to rise slowly to the surface after a short interval. On the first of such trips about a dozen fish were collected and taken back to the laboratory. These were placed in a well-aerated aquarium. At first they seemed almost dead—all lying motionless on their sides, with only an occasional movement of a fin. The next day, however, they seemed fully recovered and all were swimming about apparently quite normal. A few of these examined at this time were found to have a very heavy infestation.

In brief, the meager facts obtained on the epidemic from Nov. 27 to Dec. 10, 1947, can be summarized as follows:

1. Many calico bass and bluegills died during this period. No official estimates could be obtained, but laymen who observed the phenomenon estimated the deaths to be in the thousands.
2. One calico bass died for every ten bluegills. These were apparently the only fish affected.
3. All fish that were infested by these parasites appeared to have a heavy coating of mucus over the gills.
4. Estimated number of parasites on each fish was 250-300.
5. Age group (as determined by scale readings) was 1-2 years.

During the late fall of 1948 these observations were continued. A large fish trap was constructed and set in deep water as soon as ice covered the reservoir. All of the species of the Centrarchidae as well as one yellow perch were examined. Later in the year the fish were obtained by seining and from fishermen.

In this survey the large-mouth bass, *Micropterus dolomieu*, was found to be parasitized by a second species, *E. centrarchidarum*. This species is generally larger, broader, and found on the outside of the gill filaments, in contrast to *caeruleus* which is found between the gill filaments. In addition, there are no knobs on the inside surface of the distal end of the second pair of antennae.

Again there were morphological differences from Wilson's description of *centrarchidarum* and this phase of the work will be discussed in a later paper. Both species had the blue pigment but *centrarchidarum* was never as deeply pigmented as *caeruleus*. Strangely enough, both species had the same hair and spine formula on their appendages. This is: 1st exopod, I-0; 0-1; II-5, endopod 0-0; 0-1; II-3: 2nd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4: 3rd exopod, 0-0; 0-1; 0-6, endopod, 0-1; 0-2; I-4: 4th exopod, 0-0; 0-5, endopod, 0-1; 0-2; I-3.

In addition to the sampling of fish from Westons Mills, two other bodies of water in the New Brunswick area were sampled. These included the lower section of the Delaware-Raritan Canal and the small pond in Johnson's Park. The bluegills and calico bass in Johnson's Park were found to be free of ergasilids but the canal proved as fruitful as the reservoir. A summary of the fish examined is given in Table I.

Some interesting facts are foreshadowed in Table I. Although the amount of sampling from both bodies of water was not extensive enough to reveal fully the actual condition, nevertheless the methods by which these fish were obtained and the period of time over which the sampling was made certainly indicate the trend that one might expect to find if a more extensive sampling were to be taken.

For example, only five large-mouth bass were obtained—but under totally different conditions and at various times. The fact that all five had infestations does not indicate that all the bass are parasitized, yet one would expect to find a high percentage of the bass serving as hosts to these parasites. On the other hand, not once during this entire period of research has there ever been found a pumpkinseed infested with these copepods. Certainly one can say that for this species the incidence of parasitism is very low.

Again, viewing the information in the same light, one should expect the bluegills to be parasitized about 50% of the time in

TABLE I.

Result of the Samplings from Westons Mills and Delaware-Raritan Canal from Nov. 30, 1948-July 30, 1949.

| *Name* | *Total No. Caught* | *Percent of parasitism* | *Average Length* | *Length Range* |
|---|---|---|---|---|
| Calico bass* | 5 | 100% | 5.79″ | 4″–7″ |
| Bluegills | 15 | 60% | 5″ | 2″–7¾″ |
| Pumpkinseed | 6 | 0% | 4″ | 3″–5″ |
| Large-mouth bass | 5 | 100% | 6.4″ | 2½″–12″ |
| Yellow perch | 1 | 0% | 7″ | 7″ |

* The highest infestation noted was on one calico bass 5¾″ in length; 259 *caeruleus* were counted on this fish.

Westons Mills and the Canal. No data on calico bass could be obtained from the Canal but from the available information it would seem that these fish have become the most heavily infested in Westons Mills, not only in number of individuals but in number of parasites per fish. This is significant, for although the calico bass was found to be the most heavily infested as well as the most commonly parasitized fish, the epidemic of 1947 killed only one calico bass to ten bluegills. Unfortunately, here also, too little information is at hand. On the basis of the present data, however, there seems to be two logical explanations for this:

1. The calico bass are more resistant to the infestation of these gill parasites than are the bluegills and have been able to build up a resistance.
2. All the bluegills left are those that have built up a resistance to these parasites, or those that were only slightly parasitized.

Both fish are to be found in the same general type of environment and both have similar food habits, so apparently these two factors may be discounted.

## Pathogenesis.

There has been a great deal of controversy over the extent of damage done by the ergasilids, as well as exactly what kind is done. Wilson (1911) states that "Living as they do upon the fish's gills, there can be but little doubt that they feed upon blood." Halisch (1939) in his observations on *E. sieboldi* and *E. minor* on the gills of tench states that extra-intestinal digestion is important and that much more tissue is destroyed than is ingested by the parasitic copepod. Blood may be taken in. Fungi may grow in the lesions.

In contrast to these two observations, Henderson (1926), in her work on *E. lucioperca*rium, observed that "The gills may be heavily attacked without affecting the health of the fish. It is a harmless parasite, which, while it only benefits the unbidden guests, causes no lesions and consequently does no injury to the host." (If this is the case it should not even be called a parasite, but a commensal). She goes on to explain how, in her opinion, it is impossible for the parasites to injure the gill tissue, since the mouth parts of these organisms are too weak to pierce the gill tissue.

One might suspect that the claw-like, prehensile, second pair of antennae of the parasite is capable of at least some damage to the gill lamellae, although the mouth parts may be too small to cause any injury. However, the observations in the present studies showed no evidence of mechanical injury; neither was there any evidence of digested gill tissue or blood in the intestine of the numerous copepods examined, even in females with ovaries full of developing eggs.

We agree with Henderson (1926) that these parasites in all probability feed on the excessive mucus produced under the condition of the parasitism, or the many minute mucus or bits of organic debris and bacteria in this viscid material. However, it is altogether possible that the parasites may feed on sera, straining out the corpuscles.

A close examination of the mouth parts of these ergasilids will reveal the mandibles and second maxillae heavily fringed with setae. These would seem ideal for feeding on mucus or bits of organic debris and bacteria but hardly suitable for feeding on blood. Any pathological conditions of the gills may cause the mucus glands to secrete an excessive amount of mucus (Nigrelli, 1949). This has been especially apparent during infestations of trematode gill parasites. This condition has also been observed on many of the fish that were infested with these copepods[2]. It may be that an excess mucus secretion over the surface of the gills may lower the efficiency of the gills to absorb the dissolved oxygen in the water. Under normal water conditions when there is sufficient oxygen and all the chemical and physiological factors are in proper balance, this may not have any deleterious effects. However, if, for example, a factor such as the $CO_2$ concentration in the water should be increased, it might be sufficient to reduce the efficiency of the gills in absorbing the dissolved oxygen and so cause the fish to die of suffocation.

The highest death rate has been found among the younger fishes and it is the

[2] It must be kept in mind that the heavy coating of mucus which seems to accompany fish that are heavily infested with this parasite does not mean too much in itself. Fish that have been placed in preservative or that have died from other causes may show the same condition. Moreover, some fish that were heavily infested did not have an excess of mucus covering the gills. In such cases these fish exhibited no symptoms whatsoever and appeared perfectly normal. Apparently, there is a physiological balance here that is very delicately adjusted and which can be thrown out of balance only under certain specific conditions.

TABLE II.

Check List of the *Ergasilus* Found East of the Mississippi River.

| *Names and Synonyms* | *Hosts* | *Localities Studied* | *Remarks* |
|---|---|---|---|
| *E. caeruleus* Wilson<br>Synonyms:<br>*E. confuscus* Bere<br>*E. skryabini* Mueller | Yellow perch<br>Trout perch<br>Wall-eyed pike<br>Gray pike, Blue pike<br>Rock bass, Calico bass<br>White bass<br>Warmouth bass<br>Crappie<br>Green sunfish<br>Blue-spotted sunfish<br>Pumpkinseed<br>Bluegill<br>Lake trout<br>Cisco, White fish<br>Sucker, Long-nosed gar | Lake Mendota<br>Trout Lake region<br>Lakes Erie & Michigan<br>Oneida Lake<br>Mississippi River, Iowa | |
| *E. centrarchidarum* Wright | Rock bass, Calico bass, Large-mouth bass, Small-mouth bass, White bass, Warmouth bass, Green sunfish, Bluegill, Crappie, Pumpkinseed, Sunfish (?) Wall-eyed pike, Gray pike, Sauger, Silversides, Smelt, *Microgadus tomcod* | Lake Erie<br>Lake Michigan<br>St. Lawrence River Watershed<br>Lake Champlain<br>Black Lake, N. Y.<br>Lakes St. John & Chibogamo, Quebec<br>St. Andrew's Bay, N. B.<br>Lake Maxinkuckee, Ind.<br>Mississippi River, Iowa<br>Clewiston, Fla.<br>Woods Hole | |
| *E. chautauquaënsis* Fellows | | Lake Champlain<br>Lake Mendota<br>Fairport, Iowa | Has never been found as a parasite, but may be like *elegans* |
| *E. cotti* Kellicot | Rainbow darter<br>Sculpin—*Cottus bairdii* | Lake Erie<br>Westerville, Ohio | |
| *E. elegans* Wilson | *Ameiurus* sp.<br>Northern black bullhead<br>Channel catfish<br>Short-nosed gar<br>Long-nosed gar | Lake Okeechobee<br>Myakka River & Canals<br>Peace River, Fla.<br>Mississippi River, Ia., | Parasitic only after eggs begin developing |
| *E. elongatus* Wilson | Spoonbill cat | Mississippi River, Iowa and Illinois | |
| *E. funduli* Krøyer | *Fundulus ocellaris* | New Orleans | Salt and brackish water |
| *E. labracis* Krøyer | Striped bass | Woods Hole<br>Baltimore | Marine |
| *E. lanceolatus* Wilson | Gizzard shad | Cumberland River, Ky. | |
| *E. lizae* Krøyer | Common killifish<br>Gulf killifish<br>Broad killifish<br>Striped mullet<br>White mullet | Englewood, Fla.<br>New Orleans | Salt and brackish waters |
| *E. luciopercarum* Henderson | Pike perches | Lake St. John<br>Lake Chibogamo, Que. | |
| *E. manicatus* Wilson | Silversides<br>Smelt<br>Two-spined stickleback<br>Top minnow (*Gambusia holbrooki*)<br>*Jordanella floridae* | Englewood<br>St. Andrew's Bay, N. B.<br>Woods Hole<br>Along Atlantic Coast | Marine |

| *Names and Synonyms* | *Hosts* | *Localities Studied* | *Remarks* |
|---|---|---|---|
| *E. megaceros* Wilson<br>Synonym:<br>*E. fragilis* Mueller | Fulton cat<br>Fall fish | Oneida Lake, N. Y.<br>Mississippi River, Iowa | Found in the nasal fossae and spiracles |
| *E. mugilis* Vogt | Striped mullet | Beaufort, N. C. | Marine |
| *E. nigratus* Wilson | Large-mouth bass | Mississippi River, Iowa | |
| *E. osburni* Tidd & Bangham | Burbot | North Central States | |
| *E. versicolor* Wilson<br>Synonym:<br>*E. celestis* Mueller | Fulton cat<br>Red-mouthed buffalo fish<br>Channel cat<br>Common brown bullhead<br>Mudcat<br>Skip jack<br>Yellow cat<br>Eel cat | Mississippi River, Iowa<br>Florida<br>Lake Erie<br>Lake Maxinkuckee | |

younger fishes that would require the greatest amount of oxygen (in proportion to the gill area), due to their greater metabolic activity. At the same time it is the younger fishes that are more susceptible to attacks from disease and parasites since they are using all their available energy toward growth. Wilson states that it is the young fish that are most heavily parasitized and this is probably true—especially during an epidemic. However, larger fish may also be quite heavily parasitized. (See Table I).

The ergasilids on the large-mouth bass were never very abundant—never more than thirty on any individual. Although Wilson (1916) mentions fish fatalities from the ergasilids he does not mention which species of copepod causes death, nor which species of fish are killed. In checking all the literature on *centrarchidarum*, never were their numbers found to be as great as for *caeruleus*. Therefore, one wonders if *caeruleus* is not the only one that may appear in such numbers as to bring about the death of a fish.

This leads us to speculate on how many ergasilids must be present on a fish to cause death. It would seem that numbers that lead to the death of a fish at one time, appear to have no effect at another. However, during the epidemic of 1947 none of the dead fish had less than an estimated 250 copepods. Whether fewer parasites can bring about the death of a fish remains to be determined by further study.

It is apparent from the literature that *E. centrarchidarum* is the most widespread parasite and probably the best known. It has been found in all the main regions studied, including the marine habitat, but it has not been found on as many hosts (16) as has *caeruleus* (19), nor on as great a variety.

*Caeruleus* has not been found in all the areas that have been studied and so far has proved to be an exclusively fresh-water parasite. Additional research may also reveal that *caeruleus* is more widespread than *centrarchidarum*. It is unfortunate that most of the workers in this field have failed to make clear whether *caeruleus* has always been found between the gill filaments of its host. If it is found between the gill filaments of such clear-water fishes as the lake trout, cisco and white fish, certainly Wilson's explanation for their being found between the gill filaments is not substantiated.

*E. versicolor* is apparently third in abundance and seems to be more specific in its parasitism.

Many of the *Ergasilus* have only been found on one or a few hosts, but it is still too early to state definitely that they are specific for only those hosts.

## Conclusions.

1. It seems quite likely that *Ergasilus* may indirectly cause death to fish, although it probably seldom causes extensive damage to any given fish population.
2. Young fish (1-2 years) are apparently the only ones on which these parasites may prove fatal. Although infestations have been found to be equally high on all age groups, more young fish appear to be heavily infested than older ones.
3. Ponds where the fish are overcrowded or that are small in area seem to be the only places where infestations become high enough to cause death.
4. Ergasilids do not feed on blood, but probably on mucus or bits of organic matter found in the viscid material.
5. Death of fish is probably due to a delicate physiological imbalance affecting the diffusion of oxygen through the gill tissues.

6. *E. caeruleus* can always be distinguished from *E. centrarchidarum* by the three knobs on the second pair of antennae, and by the fact that it is always found in between the gill filaments. Variations among these copepods are exceedingly great.
7. Although Wilson considers *E. caeruleus* a parasite of the plant-eating Centrarchidae, it is also found on species that are quite carnivorous and not generally found among aquatic vegetation. It undoubtedly is found most commonly on fishes that typically inhabit an environment of aquatic vegetation, such as the bluegill and calico bass.
8. Though *centrarchidarum* and *caeruleus* have often been found on the same fish (Wilson, 1911, 16), they were never observed together in the New Brunswick area nor was *centrarchidarum* ever observed on either bluegills or calico bass in this area. Neither was observed on any but the above species of fish.
9. It may be that certain factors, chemical, physical, physiological and environmental, or a combination of these, determine which hosts may be parasitized.
10. No reason could be found to explain why the pumpkinseed, *Lepomis gibbosus*, is free from these copepod parasites in this region.

## SUMMARY.

An epizootic in Westons Mills Reservoir which caused the death of many bluegills and calico bass was investigated.

A copepod parasite, *Ergasilus caeruleus*, was believed to be the indirect cause of the death of these fish. Apparently, metabolic wastes from the copepod or irritation to the gill tissues causes an excessive secretion of mucus. This mucus may lower the efficiency of the gills, so that when certain other factors are not in proper balance the fish will suffocate.

Large-mouth bass were found to be infested with another species *E. centrarchidarum*.

A brief survey of two other bodies of water in the New Brunswick area revealed that the incidence of parasitism from these ergasilids is quite high for bluegills, calico bass and large-mouth bass, but does not seem to be present on the pumpkinseed.

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# 16.

## An Analysis of Reproductive Behavior in the Mouthbreeding Cichlid Fish, *Tilapia macrocephala* (Bleeker).[1,2]

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(Plates I-III; Text-figures 1-10).

### INTRODUCTION.

Teleosts of the family Cichlidae are noted for their elaborate patterns of courtship, mating and parental care, and for the readiness with which they breed in the restricted confines of the small aquarium. It is largely because of these attributes that cichlids have become the subjects of several extensive investigations of fish behavior. Outstanding among these studies are those of Breder (1934) on the blue acara, *Aequidens latifrons*; Noble and Curtis (1939), Peters (1941) and Seitz (1942) on the jewel fish, *Hemichromis bimaculatus*; Peters (1937) on the small Egyptian mouthbreeder, *Haplochromis multicolor;* and Seitz (1940) on a closely related mouthbreeder, *Astatotilapia strigigena.*

These students have investigated topics such as schooling, sex recognition, courtship, territory, social dominance, spawning, parental care, the stimuli causing the release of various innate responses and many other related items of behavior. In these studies, mating behavior has been described qualitatively and in varying degrees of detail. Although the reports in most cases have been based on a number of observed spawnings, the results are given in a generalized or "averaged" form and the only suggestion of variability in behavior is found in such broad phrases as "this *usually* happens," or "the *typical* mode of behavior is." Moreover, the "averaging" is often achieved by means of subjective impressions rather than in terms of a calibrated or objectively weighted evaluation of behavioral characteristics.

Variability is a fundamental characteristic of biological phenomena, a characteristic which always merits careful consideration in studies of animal behavior. It is the writer's belief that the study of teleost behavior cannot extend very far beyond the present descriptive stages unless and until methods of a more quantitative nature are employed. Students of mammalian psychology, and particularly of rodent behavior, have made excellent progress by utilizing quantitative procedures. The present study afforded an opportunity for testing the applicability of comparable techniques in the study of the reproductive behavior of fish.

The present report is concerned with the average behavior and the range of variability under constant aquarium conditions of a type which can be readily duplicated. In other investigations now in progress, the mating activities of brain-operated and hormone-treated animals will be compared to the norms obtained in the present report.

Nothing appears to be known concerning the mating behavior of *Tilapia macrocephala* in the wild state, and the present report is hardly intended as a substitute for such an investigation. Nevertheless, wherever the behavior of fishes has been studied both under field conditions and in captivity, agreement has been fairly good, as for example in the Centrarchidae. It is anticipated that the over-all picture obtained in this study should prove to be essentially similar to conditions prevailing in the natural state, and that differences if any would be expected only in some of the lesser details.

### LITERATURE.

Information concerning the breeding habits of *Tilapia macrocephala* and of related species belonging to the same genus has been furnished for the most part by aquarium hobbyists and through cursory observations by field naturalists. It is realized that because aquarists' reports often fall below generally recognized standards of scientific accuracy, as might be expected considerable confusion exists in the literature concerning certain aspects of the breeding patterns of *Tilapia.* Some of these difficulties may no doubt be attributed to an improper identification of

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the species in question, since aquarists sometimes trust the knowledge and dependability of fish dealers for the identity of their subjects. Nevertheless it is possible to obtain from this literature a rough picture of the reproductive habits of the genus *Tilapia*. For these reasons the inclusion of numerous aquarists' accounts is considered expedient. What may be offered herein is by no means intended to be a comprehensive review of the extensive popular literature.

Brief descriptions of the breeding habits of *Tilapia macrocephala* can be found in the aquarium texts of Stoye (1935), Arnold and Ahl (1936) and Innes (1944). In addition, reports on the spawning of *Tilapia heudeloti* (which according to Boulenger (1915) may be a variety of *Tilapia macrocephala*) have been presented by Breder (1934) and Schoenfeld (1934). These accounts tell us briefly that (1) a nest is built by the mating pair; (2) the female deposits the eggs in the nest; (3) the male fertilizes the eggs as soon as they are deposited; (4) shortly thereafter the male takes the eggs into his mouth; and (5) the eggs hatch and develop in the mouth of the male. How long the eggs are retained in the male's buccal pouch is not indicated, but Stoye (1935) reports two cases where eggs were carried 24 to 29 days respectively. Stoye considers these periods abnormally long as a result of excessive disturbances.

With four probable exceptions, all the species of *Tilapia* whose spawning habits have been reported are mouthbreeders. The four exceptional species remove their larvae to sand pits in typical cichlid fashion. These non-mouthbreeding species are (1) *Tilapia guineasana* (Roloff, 1938, 1939), (2) *Tilapia spaarmanii* (Hey, 1945, 1947; Anon., 1948)[3], (3) *Tilapia melanopleura* (Svenssor, 1933; Bertram, Borley and Trewavas, 1942) and (4) *Tilapia zillii* (Bade, 1923; Stoye, 1935; Arnold and Ahl, 1936; Bertram, Borley and Trewavas, 1942). However, Liebman (1933) describes *Tilapia zillii* as a mouthbreeder. Incubation of the eggs is accomplished by the females of *Tilapia flavomarginata* (Pellagrin, 1906)[4], *Tilapia galilaea* (Pellegrin, 1903, 1905), *Tilapia martini* (Boulenger, 1906), *Tilapia microcephala*[5] (Junghans, 1918) and *Tilapia mossambica*[6] (Bade, 1923; Dietz, 1926; Roloff, 1937; Peters, 1937a, 1939; Seleuthner, 1941; Hey, 1947). The same appears to be true for *Tilapia squamipinnis*, *Tilapia lidole*, and *Tilapia shirana* (Bertram, Borley and Trewavas, 1942).

The male is credited with the care of the eggs in *Tilapia dolloi* (Asch, 1939), *Tilapia heudeloti* (Breder, 1934; Schoenfeld, 1934), *Tilapia macrocephala* (Stoye, 1935; Innes 1944), *Tilapia microcephala* (Schreitmüller, 1920) and *Tilapia simonis*[7] (Lortet, 1875; 1883). However, there is some disagreement on this point since both the male and female are believed to incubate the eggs in *Tilapia simonis* (Pellegrin, 1903; Liebman, 1933), *Tilapia galilaea* (Liebman, 1933), *Tilapia microcephala* (Locke, 1932), *Tilapia nilotica* (Boulenger, 1901) and *Tilapia zillii* (Liebman, 1933). Bodenheimer (1927) claims that females alone incubate the eggs of *Tilapia simonis*, and Arnold and Ahl (1936) claim the same for *Tilapia dolloi*.

Irvine (1947) states that the male or possibly both sexes of *Tilapia discolor* and *Tilapia heudeloti* incubate the eggs, but contrary to the findings of Boulenger, Irvine relegates this function to the female in *Tilapia nilotica*. Liebman (1933) believes that it is quite general in Palestine cichlids for both parents to incubate the eggs, but the number of females performing this function is higher than the number of males so doing.

The length of the incubatory period has been reported for only a few species. Arnold and Ahl (1936) say about 14 days for *Tilapia dolloi;* Schreitmüller (1920) gives 4 to 6 days for *Tilapia microcephala;* Roloff (1937) reports 21 days for *Tilapia mossambica;* Bade (1923) offers a value of 15 days while Dietz (1926) and Seleuthner (1941) both give 13 days as the incubatory period of this species.

The retrieving into the female's mouth of newly released young has been reported for *Tilapia dolloi* (Arnold and Ahl, 1936), *Tilapia macrocephala* (Stoye, 1935), and *Tilapia mossambica* (Roloff, 1937; Seleuthner, 1941) while in *Tilapia microcephala* the male is credited with that activity (Schreitmüller, 1920).

Nest making by these mouthbreeders has received some general attention. On a number of occasions, Lortet (1883) witnessed the female *Tilapia simonis* lay approximately 200 eggs in a small excavation which she had hollowed out and cleaned in the silt among the reeds. Nest building by both the male and the female *Tilapia nilotica* was observed in the field by C. L. Boulenger (1908). Roloff (1937) describes the nest of *Tilapia mossambica* as being 20 cm. in diameter. Seleuthner (1941) reports a nest for this species which was 25 cm. in diameter and reached a depth of 4 cm. in the middle, while Hey (1947) pictures it as a "small saucer-shaped depression." Bertram, Borley and Trewavas (1942) describe the nest of *Tilapia squamipinnis* as a circular depression.

Other mouthbreeding cichlids are listed by Peters (1937) as belonging to the genera *Astatotilapia*, *Ectodus*, *Geophogus*, *Hap-*

[3] Also recorded in "Report No. 1 (1944) Inland Fisheries Dept., Union of South Africa"—1945.

[4] Designated by Boulenger (1911) as *Tilapia andersonii*.

[5] *Tilapia microcephala* = *Tilapia heudeloti*. According to Boulenger (1915, p. 178) *Tilapia macrocephala*, and *Tilapia multifasciata* "may ultimately have to be regarded as varieties of *T. heudeloti*. I am unable to find characters by which to separate them sharply."

[6] *Tilapia mossambica* = *Tilapia natalensis*.

[7] Placed in the genus *Tilapia* by Boulenger (1899) but now referred to a new genus *Tristramella* by Trewavas (1942). Lortet (1875) called this fish *Chromis paterfamilias*.

*lochromis, Pelmatochromis* and *Tropheus.*[8] It is to be noted that at least some of these genera also contain non-mouthbreeding species, suggesting a multiple origin of this habit even within the cichlid family. This problem has been considered in some detail by Breder (1933) and Myers (1939).

The small Egyptian mouthbreeding cichlid, *Haplochromis multicolor,* and a closely related form, *Astatotilapia strigigena,* have been the most popular and intensively studied of all the mouthbreeding fish. In addition to the scientific investigations previously mentioned, more than 30 accounts of the spawnings of these two fish have appeared in the last three decades, the majority of them in the Wochenschrift für Aquarien-und Terrarienkunde. These accounts, which are relatively consistent in their general implications, demonstrate that the spawning behavior of these species differs considerably from that of the various species of *Tilapia* described above. For this reason what is known about the *Haplochromis* and *Astatotilapia* mating patterns is summarized briefly for the purposes of comparison.

In these species the male does practically all of the nest building. Upon the completion of the nest, the female starts the oviposition by depositing between four and ten eggs in the nest. The male immediately fertilizes the eggs after which they are picked up by the female. This cycle is then repeated as the female lays a second batch of eggs. Between five and ten such cycles have been reported by various authors as comprising a spawning. The eggs are carried for 9 to 20 days, after which the young are released. However, the young are taken back into the female's mouth at night and at other times when disturbed. Such a retrieving of the young has been the subject of a special investigation by Peters (1937).

## Material and Methods.

*Tilapia macrocephala* (Bleeker) is native to West Africa, particularly in the region of the Gold Coast. Boulenger (1915) describes the species as coming from the Gold Coast, Ashantee and Lagos. Many of his specimens were taken from the Ancobra river and Secconda lagoon in the Gold Coast, and from the Lagos lagoon. According to Arnold and Ahl (1936) the fish is found in the brackish lagoons of the coast and the swampy deltas of rivers.

The individuals utilized in this study were selected from a laboratory-bred stock which had been maintained for a number of years prior to the start of the present research.[9] Males were chosen for the brightness of their yellow operculum which is a secondary sex character (Pl. I, Fig. 1). The females (Pl. I, Fig. 2) were selected on the basis of the complementary sex character, namely a deep red spot in the center of the gill cover.[10] These dimorphic color patterns appear at sexual maturity and disappear after castration (Aronson, in manuscript).

Pairs were established by random selection and were placed in 54-liter aquaria, 60 cm. × 30 cm. × 30 cm. each containing roughly 36 liters of water. The side and rear walls of these tanks were painted pale blue to minimize any possible disturbing influences from neighboring tanks, and also to facilitate the ability of the investigator to follow the activities of the fish. The tanks were located in a greenhouse the temperature of which was maintained throughout the year at 26° C. with a positive and negative variation of approximately 3° C. To furnish hide-outs for the fish which at the same time would not obstruct the observer's view, a mat of floating plants was placed in every tank. *Cabomba* was extensively used for this purpose, but *Sagittaria subulata* was found to be somewhat more suitable and was used whenever available.[11] The fish were fed mostly a dehydrated preparation consisting of dried shrimp, oatmeal, beef liver, lettuce and spinach. At times this was supplemented by live tubifex worms. Occasionally the fish nibbled at the stonewort *Nitella,* and this was placed in the tanks when available. The tanks were aerated continuously, and the water was changed whenever it became excessively murky. This was approximately once a month. Tap water brought to the proper temperature was used in washing the tanks and for replacement.

In order to avoid injury to the fish due to excessive nipping which often occurred after spawning, a transparent glass partition was placed in the aquarium, separating the male from the female as soon as observations of oviposition were completed. As the individual carrying the eggs (generally the male) eats little or nothing during the incubatory period, brooding fish were not fed during this interval. By the time that the young were released from the male's mouth, the females often were prepared to spawn again. However preliminary observations indicated that when such spawnings occurred males sometimes behaved abnormally, due apparently to the protracted period of inanition. To avoid this difficulty an arbitrary rule was established to the effect that males were separated by a transparent glass partition from females for one week after they had released their young or had swallowed their eggs. This interval allowed the males to feed and regain their strength. While thus iso-

[8] An older listing of mouthbreeding cichlids given by Pellegrin (1903) includes the genera *Geophagus, Acara, Chaetobranchus, Tilapia, Paratilapia, Pelmatochromis, Ectodus* and *Tropheus.*

[9] I am greatly indebted to Miss Ethelwyn Trewavas of the British Museum for kindly checking and verifying the taxonomic identity of the fish as *Tilapia macrocephala.*

[10] Examination of this spot by Aronson and Holz-Tucker (in manuscript) has revealed that it is in actuality a semi-transparent window through which the underlying red gill can be seen.

[11] The author wishes to express his appreciation to Dr. Myron Gordon of the New York Zoological Society for furnishing all of the sagittaria used.

lated, females often spawned alone but observations showed that a considerable amount of courtship took place through the glass partition.

To prevent the parents from eating their young after they were released, large masses of the stonewort *Nitella* were placed in all tanks where young were being incubated. The stonewort was distributed equally on both sides of the partition since the newly released fry could easily swim through the cracks at the intersection of the partition and the glass walls of the tank. Disturbances caused the young to swim into the fine interstices of the *Nitella* where they would not be followed by their cannibalistic parents.[12]

The criteria employed to indicate the approach of oviposition were (1) persistent nest building, mostly by the female, (2) heightened courtship activity, and (3) protruding genital tubes. When these signs were observed, continuous records were taken of the courtship and mating activities of the pair up to the time of spawning and for one-half hour thereafter. Attempts were made to secure continuous pre-spawning records for three hours. However, this goal was attained in only a small number of cases with the result that the records vary from just a few minutes before spawning up to the full three-hour span. A serious difficulty was encountered here in that the activities of many promising pairs were observed continuously for many hours up to a whole day without the fish ever ovipositing.

After the present experiment had been terminated, behavior during the interspawning interval was studied, using different pairs of *Tilapia*. The experimental conditions were the same as before with the following minor exceptions: (1) no plants were used but instead inside aquarium filters served as hide-outs; (2) the water in the tanks was never changed; (3) the males were never separated from the females. The actual spawnings of these pairs were not witnessed, all ovipositions being recorded as having occurred at the time the eggs were discovered in the male's mouth. All pairs were checked twice daily for eggs. A 15-minute record of the behavior of a given pair was taken 5 or 6 days after the spawning and again on the 15th or 16th day. The interval between successive spawnings varies from 8 days up to almost a year with a mode of 15 days (Aronson, 1945). Approximately two-thirds of the intervals are less than 29 days. Thus the 5- or 6-day score serves as an intermediate record for the shorter interspawning intervals, while the 15- or 16-day score serves in the same capacity for the longer intervals. Obviously some of the 15-day records could not be taken because of intervening ovipositions. Many of these observations served, moreover, as behavior records for varying days before spawning.

## Qualitative Description of Reproductive Behavior.

In order to furnish the reader with the proper background for the quantitative investigation, it is appropriate to present first a general description of mating activities. This account does not take into consideration the question of the range of variability and any exceptional items of behavior. Details concerning many of the generalizations made here will be considered in the next section.

Certain of the behavioral patterns which increase in their frequency of occurrence prior to spawning and which lead up to the acts of oviposition and fertilization generally are classified as courtship activity. Such behavior appears to express the level of sexual excitability of the given individual. In accordance with the views of Huxley (1914, 1938), Howard (1929) and Marshall (1936), it is assumed that courtship tends to hold the pair together, and through mutual stimulation may lead to a well synchronized spawning. In the terms of Schneirla's (1946) discussion, such relationship may be thought of as involving trophallactic processes, and the temporal aspects of these interactivities are of significance from the standpoint of adaptive function. *Tilapia* eggs (Pl. I, Fig. 2; Pl. II, Figs. 3, 4), as well as those of other oviparous teleosts, are shed in a flaccid state, but rapidly become hard and turgid upon entering the water. That is, they "water harden" (Breder, 1943). Hence, to insure fertilization the male must deposit his sperm over the eggs within a very short time after they are laid. An adequate synchronization of the pair's reproductive processes thus appears to be critically important for effective species survival.

There follows a description of the early courtship behavior of *Tilapia macrocephala*: (1) The male and female approach each other and suddenly dip their heads; or one member of the pair lowers its head. This

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12 This was the author's first experience with the maintenance of tropical fish. Since then, several innovations have been developed. Inside aquarium charcoal filters are now placed in every tank. These keep the water clean and eliminate the need for changing it. Plants are not used since they grow poorly in *Tilapia* aquaria. The food formulae have been modified as follows: (1) *Wet mash*: 2½ lbs. liver; ½ lb. chopped lettuce and spinach; ½ lb. dried ground shrimp (mostly shell); ½ lb. dried and ground refined shrimp (mostly muscle); Pablum (or other precooked infant cereal)—enough to make thick paste (approximately 3½ lbs.); 1 pinch salt. The liver is chopped, about 1 cup of water added, and the mixture is then liquefied in a blending machine. All ingredients are mixed together with sufficient Pablum to make a paste. The food is further solidified and preserved by packing into jars and immersing them in boiling water for about 10 minutes. (2) *Dry food*: 12 lbs. dried shrimp (mostly shell); 12 lbs. dried refined shrimp (mostly muscle); 10 lbs. liver; 6 lbs. chopped lettuce; 6 lbs. chopped spinach; 28 lbs. Pablum; 2 level teaspoons salt. The ground spinach and lettuce are mixed with the Pablum and cooked for 15 minutes. The liver is cut into slices and boiled for 15 minutes in a minimum amount of water and then chopped. All ingredients are mixed together and the resulting paste spread about ½ inch thick on trays. When almost completely dry, the food mixture is ground and sifted through screens of several coarsenesses.

The sexes are no longer separated after the spawning. If the fry are to be saved they are forcibly removed from the parents' mouths on the tenth day post-oviposition, and are placed in small aquaria. At this age the young do very well without further parental care, and thus, losses through cannibalism are easily avoided.

behavior has been termed "head-nodding." (2) When one member of the pair approaches the other, spreads its opercula and expands its buccal pouch, we have called this act a "throat-puff." (3) The male or female ceases swimming movements and the trunk musculature appears to quiver for a fraction of a second. We have named this a "body-quiver." (4) When one member of the pair slaps the other with its tail, this has been called a "tail-slap." Included in this category were the frequent cases where tail-slapping motions were quite distinct, but where actual contact with the partner was not made.

Closely associated with the courtship acts, but displayed as well in many pairs throughout the interspawning interval, is a mode of behavior which we have termed "nipping." This occurs when a fish swims after its partner, and then with a sudden dart nips or bites the body of its mate. Nipping also occurred at times without a previous chase. Sometimes the male and female may nip each other simultaneously and occasionally they may even lock jaws. Frequently observed cases in which the pursuing fish darts ahead but misses the fleeing opponent also have been included under the general heading of nipping.

In addition to its association with courtship and spawning, nipping behavior appears to be related to the establishment of social hierarchies and the formation of territories. These further relations of nipping have not as yet been investigated.

The above-mentioned patterns of behavior usually appear as quite distinct, but occasionally they tend to merge into one another, so that discretion on the part of the observer is often called for in assigning a particular courtship act to its proper category. Oftentimes two or more courtship acts may be displayed in rapid succession, a frequent combination being a head-nod, throat-puff and body-quiver. Another commonly occurring combination is the throat-puff and tail-slap.

Readers acquainted with the courtship behavior of other cichlid fishes will readily recognize the resemblance of the *Tilapia* pattern with those of other cichlids. Reactions such as the body-quiver, the throat-puff and the tail-slap in some form seem to be prevalent throughout the family.

Nest-building is first observed after intensive courtship has been in progress for several hours or days. Most of this activity is conducted by the female who begins scooping up mouthfuls of gravel from scattered locations in the bottom of the tank. Soon the excavating is confined to one location, and the construction of a nest begins. Often two or more nests are constructed prior to the spawning, and sometimes nests are built and then destroyed during the construction of an adjoining nest. The nests are most often round or slightly oval. If the gravel substratum of the aquarium is not too thick, the fish dig down to the slate bottom of the tank. If, however, the depth of the gravel is more than 2 or 3 cm., the nests do not reach the slate.

In our study the length of time taken to complete a nest varied considerably from as little as one-half hour up to what appeared to be several days. In the latter case, the nest-building activity occurred in spurts, followed by periods of quiescence. The rapid builders generally worked continuously until the nest was completed. A small amount of nest-building was accomplished by sweeping movements of the tail and pectoral fins. However, this has been interpreted as incidental to swimming and balancing movements and not directly related to nest building.

After the nest is more or less completed, nest-building decreases considerably and is supplanted to some extent by nest-cleaning (Pl. I, Fig. 1) in which the female, and occasionally the male, pick continuously at the bottom of the nest. Nest-building and nest-cleaning are always interspersed among various phases of courtship responses.

As the nest takes form, the genital tubes of the male and female become more prominent. At this time, the male begins to swim slowly over the nest, rubbing his genital tube over the bottom. We have called this "passing-nest." Later when the female completes the nest, she likewise "passes-nest." Thus the pair circle around and around, rubbing their genital tubes over the nest. This behavior is often interrupted by periods of courtship, nest-building and nest-cleaning activity. As soon as a fish starts passing-nest, the genital tubes become fully erected, but if this activity ceases for a time, the tubes generally recede somewhat. This suggests that mechanical stimulation is one factor causing the erection of the genital tube. Since fish not on the verge of spawning are sometimes seen with partially extended genital tubes, other stimuli seem to be involved in the partial erection of the genital tubes. Courtship activity and hormones are suggested as possible factors.

After the passing-nest behavior of the male and female has been in progress for some time, the female stops in the nest during a "pass-nest," and her body musculature quivers for a second or two. This has been called a "spawning-quiver." Males also exhibit spawning-quivers, but in the male these responses generally are less distinct and are seen less frequently.

Spawning-quivers were the final prespawning acts and indicated the imminence of the oviposition. During one of these quivers a batch of approximately 10 to 20 eggs is extruded by the female in what we have termed an "oviposition movement" (Pl. I, Fig. 2). The female then swims just past the nest. She is followed by the male who passes-nest, usually rubbing his genital tube over the newly laid eggs and sometimes exhibiting a spawning-quiver. This complementary act has been termed a "fertilization movement" (Pl. II, Fig. 3). Sperm

apparently are emitted at this time, although no male products were apparent in our observations. The female then repeats her oviposition movement which is followed closely by a second fertilization movement of the male. After two to four such egg-laying cycles, the female swims rapidly from the nest for a distance of 15 to 30 cm., then faces the nest. Meanwhile the male swims in the vicinity of the nest for a minute or so, then rapidly picks up the eggs with his mouth (Pl. II, Fig. 4; Pl. III, Fig. 5).

In our investigations there were a few exceptional cases where the male did not pick up the eggs. Then the female nipped and tail-slapped the male violently, exhibited some courtship behavior, and finally after 10 to 20 minutes of this activity she picked up the eggs and carried them in her mouth (Pl. III, Fig. 6). We found that at times, because of the unequal sizes of the male and female, all the eggs could not fit into the male's mouth, the female would pick up the remaining eggs, but not until 10 to 20 minutes had elapsed.

Post-spawning activity consists for the most part in poking around the nest, first by the male, and later by the female as well. If any of the eggs are missed when the original spawn was picked up, they are almost always recovered during this poking activity.

After several minutes, this poking behavior sometimes gives way to extensive nipping and mouthing in which one member of the pair, generally the female, soon dominates and the other retreats into hiding.

The eggs hatch in 5 days and are carried from 2 to 15 days further, during which time the embryos continue to develop. The young are released abruptly and most of them are sufficiently developed at this time to suggest that further parental care would not be advantageous to them. Parental care appears to end suddenly with the release of the young. In fact, parents sometimes eat their newly liberated offspring. Never did we see the young swim back into the parental mouth as has been described by some authors for this and other *Tilapia* species, and which is such a striking characteristic of the small Egyptian mouthbreeders, *Haplochromis multicolor* (Peters, 1937).

With this brief description of the mating pattern we turn now to an analysis of the actual counts made of the frequency of occurrence in relation to the time of spawning of many of the behavioral acts described above.

## Analysis of the Mating Pattern.

For the purpose of analyzing the data, records were organized in the following manner. For each observed spawning, the time of appearance of the first batch of eggs was designated as the zero minute. The 15-minute period just prior to the zero minute was called the first pre-spawning interval. The period 15 minutes to 30 minutes prior to the zero minute was named the second pre-spawning interval. Twelve pre-spawning intervals were similarly measured. Again starting from the zero minute, the 15-minute interval which followed was called the first post-spawning interval, and a second post-spawning interval was likewise measured. The number of times that the various courtship and mating activities (tail-slaps, passing-nest, etc.) were recorded during each 15-minute pre- and post-spawning interval was determined for both the males and the females for all observed spawnings. With data assembled in this manner, a series of distributions was obtained (one of each behavior pattern of both the male and female for each interval). Almost all of these were strongly skewed to the right. The arithmetical mean obviously is a poor representation of the central tendency of a markedly skewed distribution. Medians are generally more suitable, but a better method of treating such data is to employ a transformation. In many cases by use of the transformation $X = \sqrt{x}$, binomial distributions were obtained which could be treated as normal curves.[13] These were checked by plotting cumulative distributions on arithmetic probability paper. However some of the distributions were not normalized following the above transformation, but approximated closely the Poisson series. This was particularly true with infrequently occurring items, where the highest frequency was zero and where the mean was considerably smaller than one. Theoretical Poisson distributions were calculated from Pearson's (1914) tables and the goodness of fit of the actual distributions was tested by the chi-square method.

Still other distributions did not approximate either the normal or Poisson series. As will be noted later, these were not subjected to further statistical analysis.

For the normal distributions, the means, range, theoretical range ($M \pm 3\sigma$), standard deviation and standard error of the mean were calculated. These were plotted graphically in a time sequence, using the method of comparing ranges and means developed by Dice and Leraas (1936) as modified by Simpson and Roe (1939). Since the length of the pre- and post-spawning records varied inadvertently for each spawning, the calculated means for each interval are based upon a varying number of spawnings. Simpson and Roe (1939) point out that the method of Dice and Leraas is less reliable when the frequencies and standard errors of the mean vary greatly. Therefore, in critical cases where the graphic method was suspected of being inaccurate, P values were calculated. The solid lines in Text-figs. 1-6, 8 and 9, indicate females; the broken lines males. The heavy vertical lines designate actual ranges of the distributions. The adjacent light vertical lines indicate theoretical ranges ($M \pm 3\sigma$). The large dots represent the means, while the short horizontal lines above and

[13] The writer wishes to acknowledge the aid given by Dr. Charles P. Winsor in suggesting the use of this transformation.

below the means indicate the range of M $\pm 2\sigma_M$. When these ranges overlap, it may generally be assumed that the differences between the means are not significant. Conversely, if M $\pm 2\sigma_M$ do not overlap, the differences between the means are significant. The limitation of this method has already been noted.

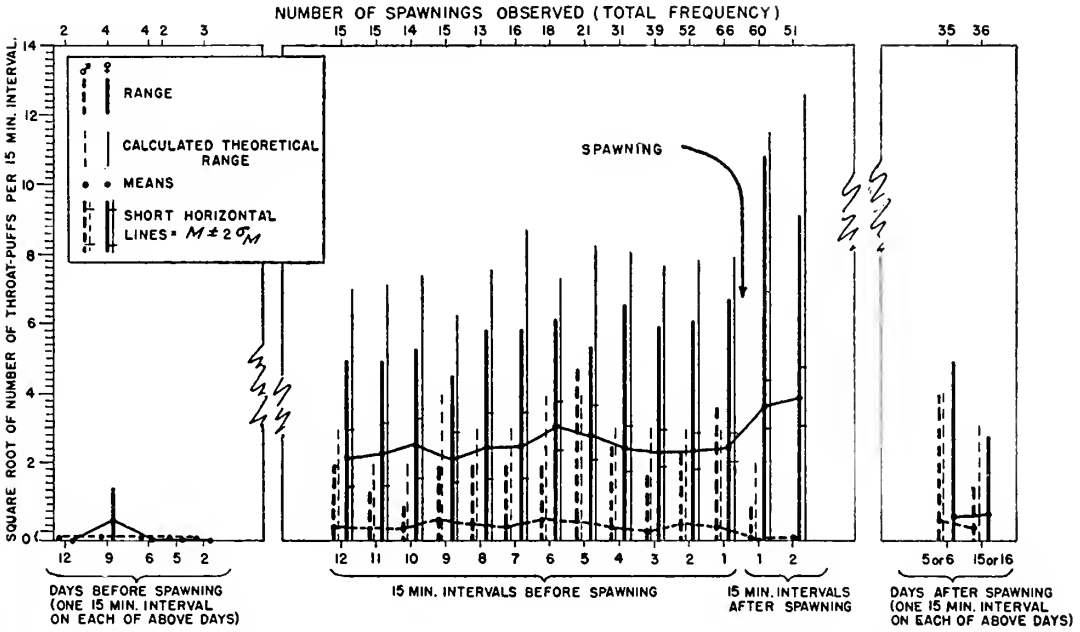
For the Poisson series, the theoretical ranges were considered to run from zero to that value of the variate having a relative frequency of .003 or less. Means were compared by the method described by Snedecor (1946). Because of the asymmetrical nature of the Poisson distribution the graphical method of comparing means described above cannot be used. Hence, in the following graphs, the range of M $\pm 2\sigma_M$ are not indicated for the Poisson distributions.

Where the distributions did not conform reasonably well to either a normal or Poisson series, only the means and actual ranges are presented on the graphs.

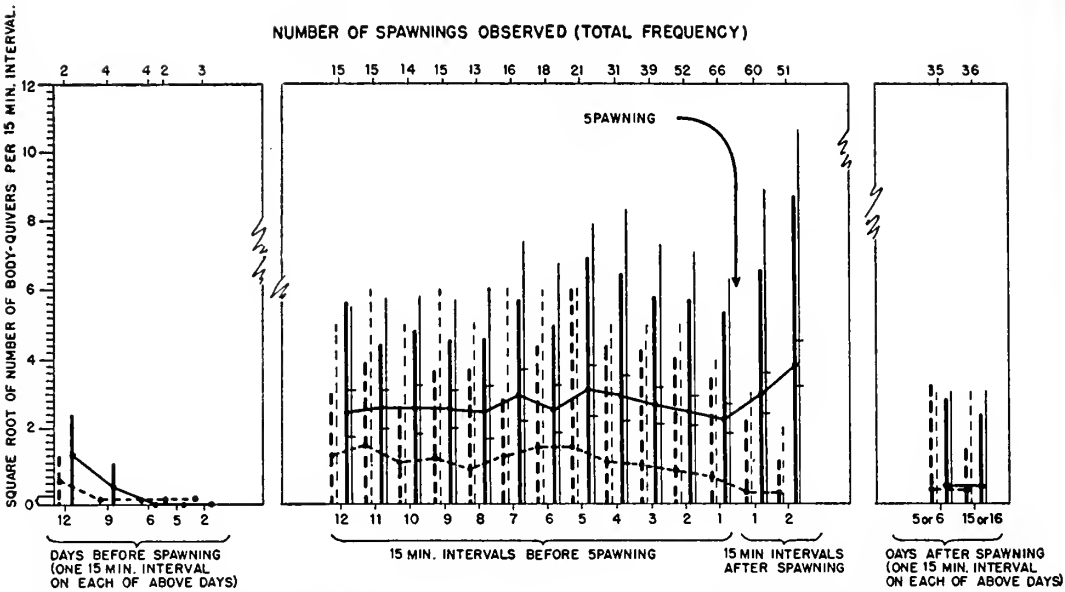
The 15-minute records on the 5th or 6th post-spawning day and on the 15th or 16th day were treated in a similar manner. Since a number of pairs spawned again within two weeks after these observations were made, it was possible to use some of these data as records of behavior on the 2nd, 5th, 6th, 9th and 12th pre-spawning days. Because of the small number of cases, only means and ranges are indicated graphically.

THROAT-PUFFS. As seen from the graph in Text-fig. 1, the females (solid lines) exhibited this behavior very rarely on the several days they were observed before the spawning. One female throat-puffed just once on the 9th pre-spawning day. However, by three hours before spawning, the throat-puffing frequency had reached a rather high level, which was maintained with little fluctuation right up to the spawning. Immediately after the egg laying, throat-puffing activity increased sharply. To be sure that this rise was not due to chance fluctuation, the means of the first pre- and post-spawning intervals were compared and were found to differ significantly ($P < .01$).

The males showed the throat-puffing behavior much less frequently than the females (Text-fig. 1, broken lines). On the several days the pairs were observed prior to the spawning, no throat-puffing by the males was seen. At three hours before the egg laying, a low frequency of throat-puffing was recorded, and this level was maintained up to the spawning. When these data were treated by utilizing the transformation $X = \sqrt{x}$ as already described, the frequencies of male throat-puffs were found to be distributed in a Poisson fashion with zero the highest frequency, an indication that the mean frequencies were less than one. This raised the question whether the males of just a few pairs were responsible for the bulk of the throat-puffing activity. A partial answer to this question was obtained by selecting the 25 spawnings in which continuous records for the first hour before spawning were available. It was found that during this hour, 64.0% of the males exhibited no throat-puffing at all. This contrasts with the figure of only 4.0% for the female. Similarly, in the seven pairs where continuous records for the first two pre-spawning hours were available, 57.1% of the males did not throat-puff. From this we may conclude that a consider-




TEXT-FIG. 1. Fluctuation in male and female throat-puffing behavior before and after spawning.



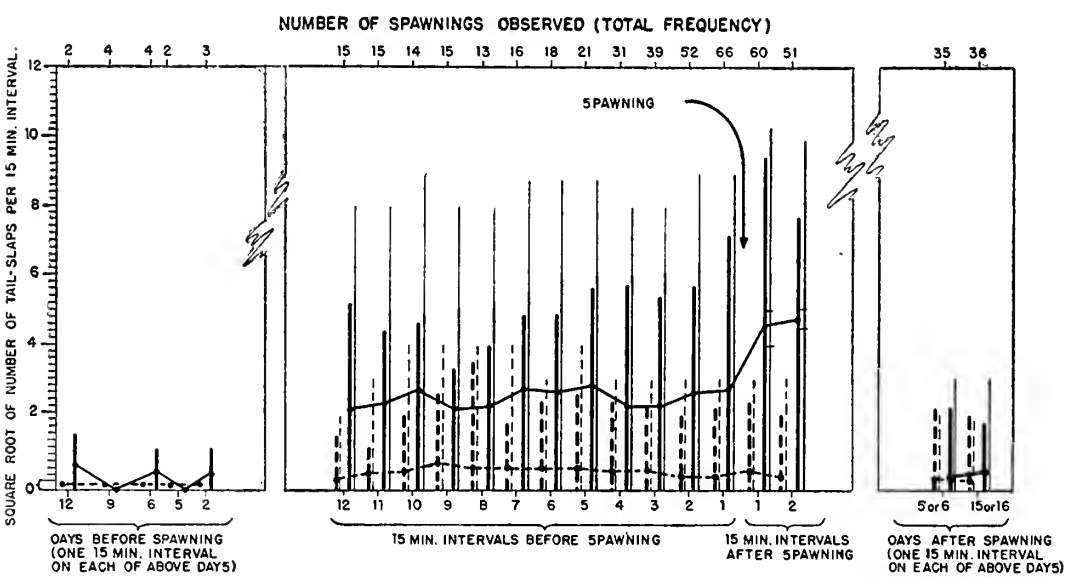

TEXT-FIG. 2. Fluctuation in male and female body-quivering behavior before and after spawning.

able number of males exhibited little or no throat-puffing behavior prior to the spawning.

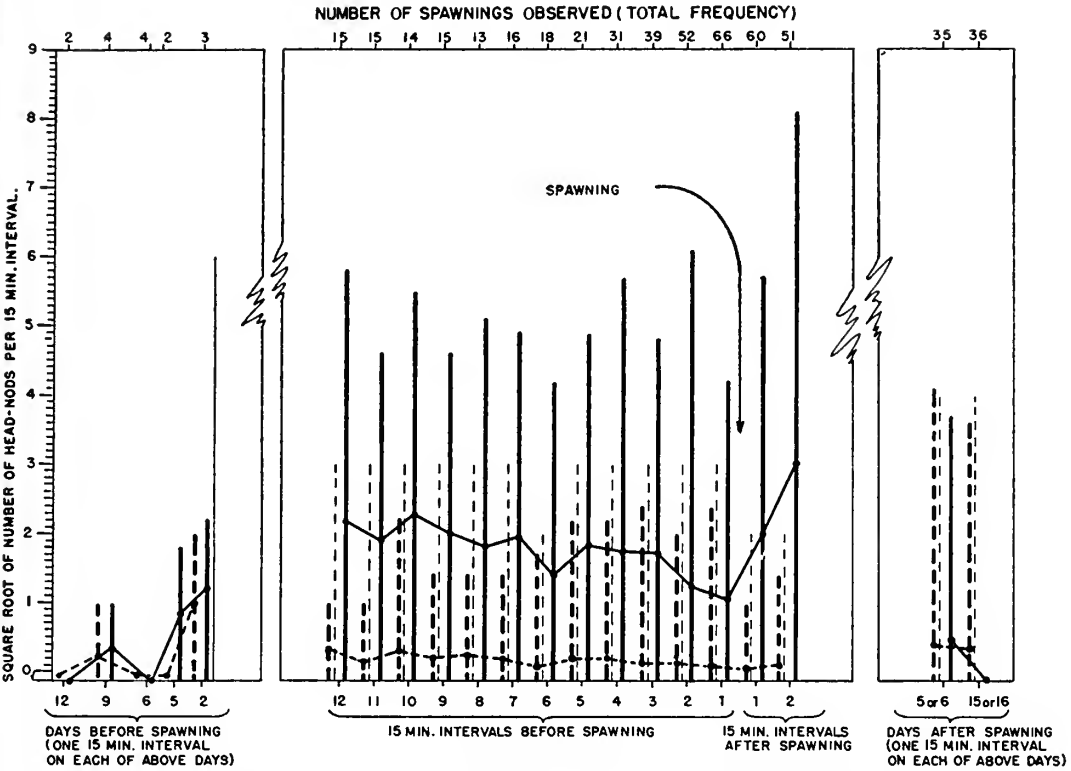
Immediately after the egg laying, throat-puffing by the male was no longer observed. Since the mouths of the males were now filled to capacity with eggs, it seems better to say that after the spawning throat-puffing could not readily be identified. By the 5th or 6th post-spawning day, many of the males were no longer carrying eggs, and now the throat-puffing behavior had reached the pre-spawning level.

BODY-QUIVERS. Only an occasional body-quiver was exhibited by the males and females on the several days they were observed prior to the spawning (Text-fig. 2), but by three hours before oviposition the body-quivers (solid lines) were very frequent occurrences in the female. They remained at this relatively constant level until the spawning, after which there was an abrupt rise. The means of female body-quivers for the first pre- and post-spawning intervals were compared, and the latter were found to be significantly higher ($P = .021$). At five days after spawning the females' body-quivering had dropped far below the immediate pre-spawning level, and remained the same during the observation period on the 15th or 16th day.

The body-quiver frequency of the males at




TEXT-FIG. 3. Fluctuation in male and female tail-slapping behavior before and after spawning.




TEXT-FIG. 4. Fluctuation in male and female head-nodding behavior before and after spawning.

three hours before spawning was considerably less than the females' and again these data were best treated as Poisson distributions. The behavior remained at this level until the fifth pre-spawning interval when it started to slope off, reaching a minimum at the first pre-spawning interval. However, when the male body-quivers of the fifth and first pre-spawning intervals were compared, this slope appears not to be significant ($P > .10$). On the 5th or 6th post-spawning day, and on the 15th or 16th post-spawning day, the body-quiver frequency of the males was very close to that of the females.

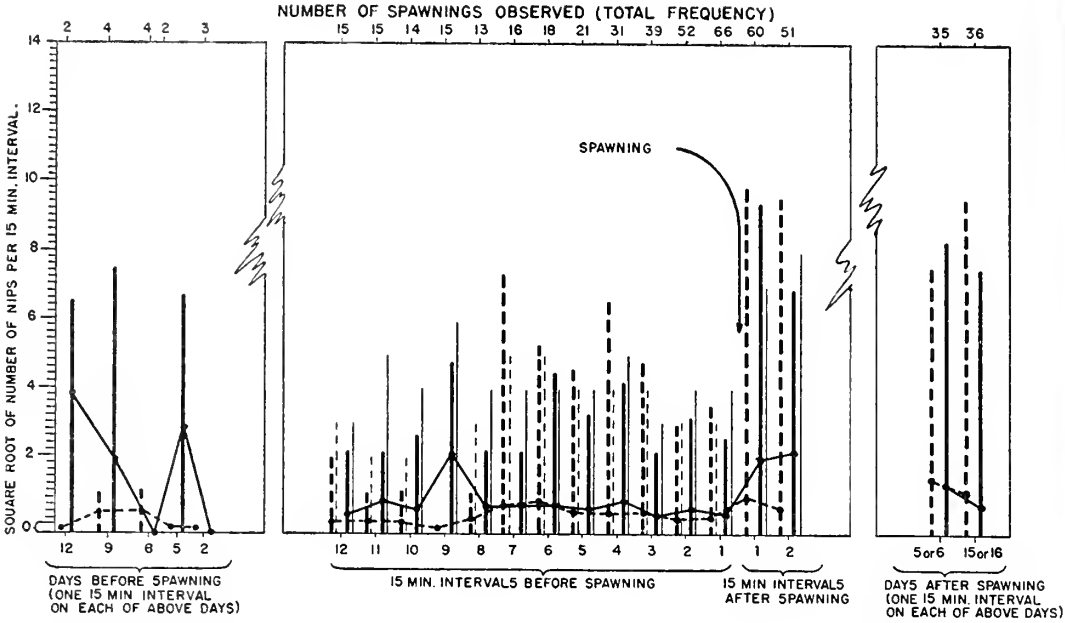
Of the 25 spawnings in which continuous records were available for one hour before the spawning, 100% of the females and 80.0% of the males exhibited body-quivering at least once. In the seven ovipositions in which continuous two-hour pre-spawning records were taken, 100% of the males gave body-quivers at least once. Thus while this courtship pattern is exhibited more frequently by the females, practically all males show some body-quivering activity prior to the egg laying.

TAIL-SLAPS. With the transformation previously described, the data of both the male and female were found to be distributed in a Poisson fashion, excepting the first two post-spawning intervals of the female which were normally distributed (Text-fig. 3). On the several days prior to the spawning occasional tail-slapping by the female was observed, but at three hours before the egg laying, the occurrence of this behavior had increased considerably. This level was maintained until the spawning, when there was another significant rise ($P < .01$) during the first post-spawning period.

No tail-slapping by the male was observed on the several days prior to the spawning, and during the three-hour pre-spawning interval, the frequency of tail-slaps remained low with relatively little fluctuation. Approximately this same frequency was observed during all the post-spawning observation periods.

Of the 25 pairs for which continuous records for the first hour were obtained, 100% of the females were recorded as tail-slapping at least once, but only 48% of the males. In the seven spawnings with two-hour continuous pre-spawning records, 71.4% of the males tail-slapped at least once.

HEAD-NODS. Following the transformation, head-nodding data for the female was characterized by a large number of zero frequencies and a small number of rather high frequencies. These did not fit Poisson distributions. At times, head-nodding was not clear cut and easy to recognize, and it is possible that a considerable amount of head-nodding passed unrecognized. Before the spawning, head-nodding activity was quite high (Text-fig. 4), at least for some of the




TEXT-FIG.5. Fluctuation in male and female nipping behavior before and after spawning.

females, and there was a still further rise after the egg laying.

The data for male behavior fit Poisson distributions quite closely. The low mean values indicate that this behavior occurred rather infrequently, and little fluctuation was noticeable before or after the spawning.

Of the 25 ovipositions from which continuous records were taken for the first pre-spawning hour, 84.0% of the females and only 20.0% of the males exhibited head-nodding at least once. Similarly, of the seven pairs where two-hour records were available, 100% of the females and 28.6% of the males head-nodded at least once. We may conclude that head-nodding is a typical female activity and that a small fraction of the males head-nod occasionally.

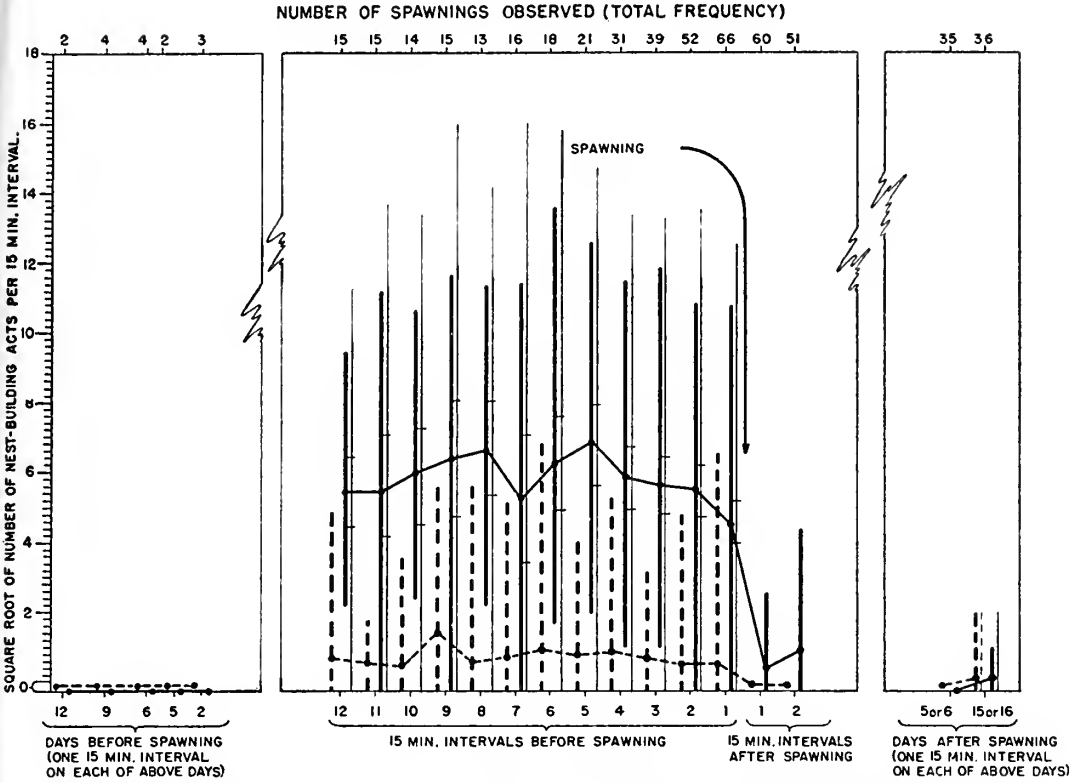
NIPS. Nipping data of both the male and female were treated as Poisson distributions. Both sexes displayed some nipping behavior on the several days they were observed before the spawning (Text-fig. 5). During the three-hour pre-spawning observation period, approximately the same amount of nipping was shown by both the males and females. After the egg laying there was a significant rise ($P<.01$) in the nipping frequency of the females. The rise in female nipping during the ninth pre-spawning interval may be significant ($P = .05$), but it was mostly due to a marked spurt of activity of a single female.

Analysis of the 25 spawnings where complete records for the first hour before spawning were taken showed that 68.0% of the females and only 28.0% of the males exhibited nipping behavior at least once. Where two-hour continuous records were available, 100% of the females, and 57.1% of the males engaged in some nipping activity. This suggests that practically all of the females and at least half of the males do some nipping before spawning.

NEST-BUILDING ACTS. On the several days before spawning, nest-building by either the male or female was not observed (Text-fig. 6), but by the third hour before oviposition, female nest-building activity had reached a rather high frequency. Since the presence of a nest and the occurrence of nest-building behavior was one of the more important criteria used to determine the imminence of spawning, and hence to ascertain the appropriateness of starting the observation, these data are likely to be somewhat biased in favor of early nest-builders. Actually at three hours before spawning, the average nest-building activity of the female may not be as high as that indicated by the data.

The drop indicated in the seventh pre-spawning interval appears not to be significant if the nest-building values of the fifth and seventh intervals are compared ($P = .13$). On the other hand, there is a noticeable downward slope between the fifth and first pre-spawning intervals, and when these two intervals are compared, the difference was found to be highly significant ($P<.01$). It is clear that female nest-building behavior drops off as the time for the laying of the eggs approaches, and it is gradually superseded first by nest-cleaning behavior (which is clearly distinguishable from nest-building), and secondly by nest-passing activity, which, as we shall see in the next section, is increasing as the nest-building frequency is declining.

Following the oviposition episode, nest-building activity dropped to a very low fig-




TEXT-FIG. 6. Fluctuation in male and female nest-building behavior before and after spawning.

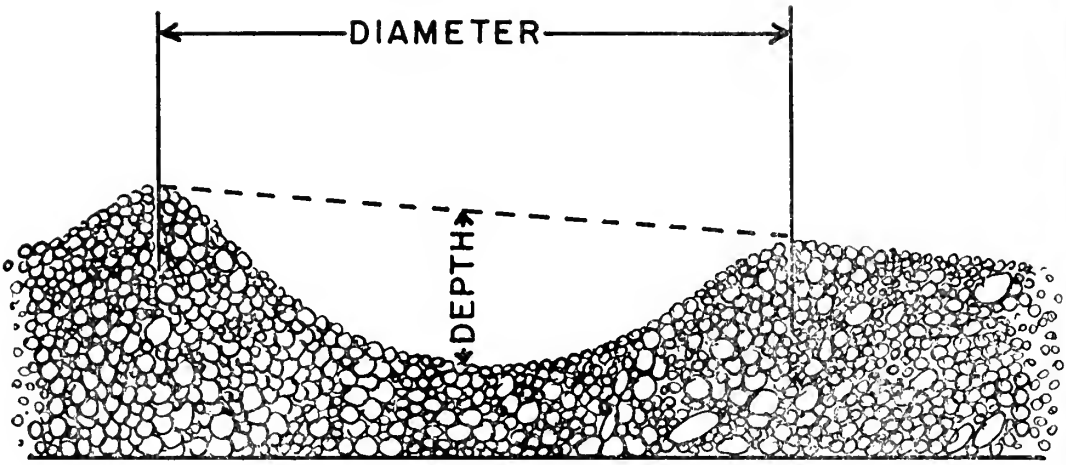
ure. On the 5th or 6th day nest-building by females was not observed, and on the 15th or 16th day only one nest-building act was observed during the 15-minute observation interval by one female out of thirty-six.

The data for the male was characterized by high frequencies of zero values and low frequencies of high values which nevertheless did not fit Poisson curves even after the aforementioned transformation. In contrast to the extensive nest-building activity of the female, that of the male was quite limited. Similar to the female, there is a downward slope in activity between the fourth and first pre-spawning intervals. However, the decline is not very pronounced and its statistical validity could not be readily ascertained. After the spawning the males no longer engaged in nest-building except for a single male which on the 15th post-spawning day nest-built four times during the observation interval. This male was paired with the one female, which was also observed to build a nest during the 15-day post-spawning interval. Two nests were present in the tank and it is apparent that this pair was approaching another spawning cycle.

Turning again to the 25 spawnings with continuous records for the first pre-spawning hour, it was found that 100% of the females and 72% of the males engaged in nest-building at least once. Of the seven pairs with continuous two-hour pre-spawning records, 71.4% of the males did some nest-building. It is probable that only a small percentage of males do not engage in any nest-building prior to the spawning.

Fifteen nests built by ten pairs were measured shortly after the spawnings. In each case the fish were first carefully removed without damaging the nests. Since in many cases the nests were oval, two diameters were taken, namely the short diameter, and at right angles to this the long diameter. The points used in these measurements are indicated in Text-fig. 7. The average short diameter was 11.8 cm., the average long diameter 13.2 cm., and the average depth 2.6 cm. The female fish (which as shown above are primarily responsible for the construction of the nests) varied from 10.7 gr. to 19.2 gr. with an average of 15.1 gr. The males were slightly heavier, weighing on the average 18.0 gr. There was no indication from these limited data of a correlation between size of fish and size of nest.

PASSING-NEST. The earliest nest-passing by the female was recorded for the eleventh pre-spawning interval, two and one-half hours before the egg laying (Text-fig. 8). Following the previously mentioned transformation, the data for this interval fit a Poisson distribution. The same is true for the records of the 6th, 8th, 9th and 10th intervals. The data for the 2nd to 5th and the 7th intervals consisted of a series of zero or very low frequencies and a smaller group of relatively high values, vaguely suggesting

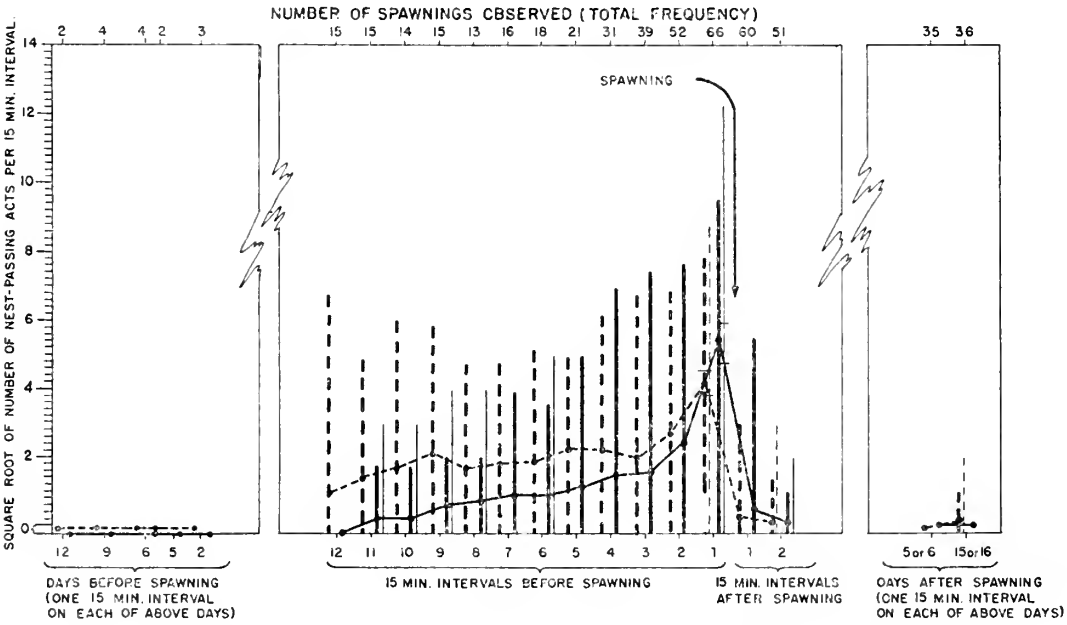



TEXT-FIG. 7. Diagrammatic section through typical *Tilapia* nest showing points used for nest measurements.

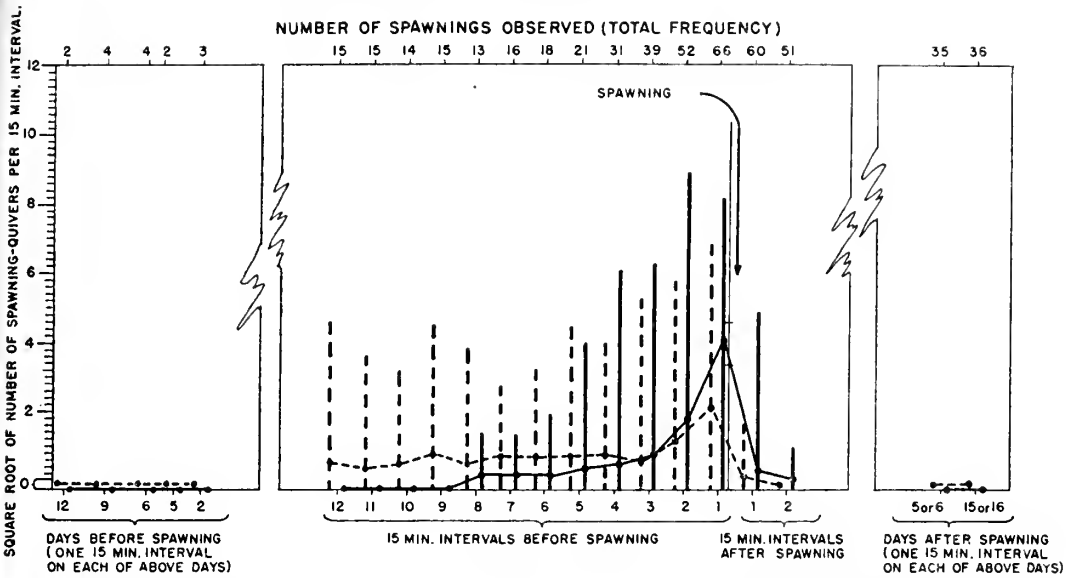
bimodal curves. The data for nest-passing for the first interval were normally distributed. These data indicate a gradually rising frequency of nest-passing as the spawning approached, with a sudden spurt of activity during the second and first intervals. After the egg laying, nest-passing activity of the female dropped to almost zero and none was recorded on the 5th or 6th and 15th or 16th days.

The nest-passing data of the male were normally distributed for the first interval. The records for the remaining pre-spawning intervals were highly skewed to the right with highest frequencies zero, which, however, did not fit Poisson series. While no nest-passing was recorded for the males on the several days prior to the spawning, a substantial amount of nest-passing was observed by three hours before the egg laying. This level of activity remained fairly constant until the second interval when it started to rise precipitously. However, during the first pre-spawning interval, the nest-passing activity of the female surpassed that of the male for the first time ($P<.01$). After the spawning, the frequency dropped to almost zero and nest-passing was not observed on the two post-spawning observation days.

Observations indicated that male and female nest-passing were not entirely independent of each other, and calculation of the




TEXT-FIG. 8. Fluctuation in male and female nest-passing behavior before and after spawning.




TEXT-FIG. 9. Fluctuation in male and female spawning-quiver behavior before and after spawning.

coefficient of correlation for the first pre-spawning interval yielded an r of + .63. This was transformed to Z = + .74 which is a highly significant correlation ($P<.01$). The nest-passing data for the remaining pre-spawning intervals appear to be comparably correlated, but the data do not readily lend themselves to this type of statistical treatment. Prior to the spawning, all of the males and females exhibited some nest-passing activity.

SPAWNING-QUIVERS. This behavior was not observed during the observation periods on the several days before the spawning (Text-fig. 9). Female spawning-quivers were first seen during the 8th pre-spawning interval, 1¾ to 2 hours before the egg laying. Their frequency gradually increased and reached a peak during the first pre-spawning interval. There was a marked drop to almost zero after the egg laying, and on the 5th or 6th days and 15th or 16th days none were seen.

A few male spawning-quivers were in evidence during the 12th pre-spawning interval, and a low level of this behavior was maintained until the second interval, 20 to 15 minutes before the egg laying, when there occurred an abrupt rise in frequency which terminated during the first interval. During the first post-spawning interval, a very few spawning-quivers were recorded, and none were seen thereafter. While a few of the males exhibited spawning-quivers long before the females, the peak of spawning-quiver activity of the females during the first pre-spawning interval was considerably higher than that of the males. However, the data did not permit further statistical analysis.

Selecting the 25 spawnings for which continuous records for the first hour before oviposition were available, it was observed that 96.0% of the females and 72.0% of the males showed at least one spawning-quiver during this hour. Similarly, in the seven spawnings for which two-hour continuous records were available, 100% of the females and 71.4% of the males were recorded as performing at least one spawning-quiver during these two hours. It thus appears that while all the females showed this behavior, in about a fourth of the males spawning-quivers could not readily be distinguished from nest-passing behavior. Since all of the females exhibited spawning-quivers and because of the sharp peak in the frequency of occurrence of this activity just before the spawning, this behavior can also be employed as an indicator of the approaching oviposition.

OVIPOSITION AND FERTILIZATION. The behavioral patterns considered thus far were recorded in terms of the number of times that the acts occurred during a short interval of time (i.e., 15 minutes), and the relative infrequency of some of this behavior accounts in part for the marked skewness of the distribution curves. On the other hand, the oviposition data which follow, and the data concerning the reactions of the male and female to the eggs and young, are based upon the total frequency of the behavior during a given spawning, and as might be anticipated, these data approximated more closely binomial distributions which could be treated as normal curves.

A nest-passing act by the female during which eggs were oviposited was counted as a single oviposition movement. A nest-passing act by the male when eggs were present in the nest was recorded as a fertilization movement. Actual contact with the eggs was not considered essential as a criterion for a fertilization movement, although in most

instances the male rubbed his genital tube over some of the freshly laid eggs.

In 76 observed spawnings, the mean number of oviposition movements by the female was 3.41 ± .13 with a standard deviation of 1.1 movements. The mean number of male fertilization movements was 3.46 ± .15 with a standard deviation of 1.3. The difference between the means is .05 ± .2 which indicates clearly that the number of oviposition movements of the female does not differ significantly from the number of fertilization movements of the male. Finally, there is a significant positive correlation ($r = +.48$, $z = +.52$, P calculated from $\frac{z}{\sigma z} < .01$) between these two activities, indicating that the number of times the males fertilize the eggs is partly related to, and probably dependent upon the number of oviposition acts of the female.

PARENTAL BEHAVIOR. In a total of 76 observed spawnings, the male alone picked up the eggs in 62 cases (81.8%), the female picked up the eggs in 6 cases (7.9%) while both male and female participated in this activity in 8 cases (10.5%).

The time after the beginning of oviposition for the male to start picking up eggs varied from 20″ to 2′10″ with a mean of 1′3″ ± 3″ and a standard deviation of 23″. For the female this interval varied from 3′18″ to 11′14″ with a mean of 7′59″ ± 1′22″ and a standard deviation of 3′17″. The difference between the means of these two distributions is obviously significant, and from these data we may conclude that the male starts to pick up the eggs as soon as the oviposition has terminated, while the female allows several minutes to elapse before she will collect any of the eggs still available. Here then is an apportioning mechanism which results in the observed fact that the male usually incubates the eggs, and the female does so on infrequent occasions.

Eggs remain in the nest available to the female under two circumstances. First, if the male's mouth is of insufficient size to contain all of the eggs, a few may be left over in the nest. This was the situation in case 1 (Table I) where a small male was paired with a large female. It was quite clear to the observer that in this instance not all of the eggs could fit into the male's mouth. Secondly, eggs would be available to the female when the male behaved atypically and did not touch the eggs. In three of these cases males had released broods seven to twelve days previous to the spawnings, and this may be a contributing factor causing the lack of response of the males to the eggs.[14] In most instances where the eggs remained in the nest for any length of time, the females would chase, nip and court the males. In a few cases, the latter retaliated and violent fighting ensued; as a result the nests were destroyed and the eggs scattered. In cases 3, 6, and 7 (Table I), as soon as the female began to pick up the eggs, the males followed suit and both gathered up the eggs simultaneously. The typical pattern when eggs are left in the nest may be summarized as follows:

(1) Immediately after the eggs are oviposited and inseminated, there is often a period of extreme quiescence lasting a minute or two.

(2) This is followed by a period in which the female appears to be inhibited from approaching or touching the eggs, but at the same time she seems to be excited by the eggs, resulting in active nipping, chasing and courting of the male who sometimes responds similarly.

(3) After several minutes the inhibitory action of the eggs begins to diminish; the female now approaches the nest, pokes around the eggs, and eventually picks them up. It was at this time that several of the recalcitrant males listed in Table I also approached the nest and in a few cases started to pick up eggs ahead of the female.

It is suggested that in cases 2 to 8 (Table I), chasing, nipping and courting by the female, and also her poking around the nest, sufficiently stimulated the male to pick up the eggs, thereby completing the pattern.

Once started, the length of time it took for males to gather up the spawn varied from 2″ to 1′45″ with a mean of 13″ ± 2″ and a standard deviation of 16″. The high variability noted here is a result of two exceptional cases, one where the male took 1′7″ and in the other 1′45″. In the remaining 60 spawnings, the time was less than 46″. On the other hand, six females took from 35″ to 3′ with a mean of 2′6″ ± 22″ and a standard deviation of 51.7″. Thus we see that not only does the female wait longer before starting to pick up the eggs, but once started she performs this task at a significantly

TABLE I.

Time from the Beginning of Oviposition for Eggs to Be Picked Up. Eight Cases Where Both Male and Female Engaged in This Activity.

| | Male | | Female | |
|---|---|---|---|---|
| Case No. | Start | Finish | Start | Finish |
| 1 | 25″— | 50″ | 7′15″— | |
| 2 | 11′00″— | 11′30″ | 6′50″— | 10′10″ |
| 3 | 3′00″— | 4′00″ | 2′30″— | 4′00″ |
| 4 | 4′05″— | 4′30″ | 4′15″— | 4′30″ |
| 5 | 2′05″— | 5′00″ | 4′30″— | 5′00″ |
| 6 | 4′10″— | 5′10″ | 4′10″— | 4′55″ |
| 7 | 6′24″— | 10′30″ | 5′50″— | 6′36″ |
| 8 | 3′50″— | 4′00″ | 1′25″— | 3′30″ |

[14] On the other hand, recent observations by Aronson and Holz-Tucker (unpublished) reveal that males in the process of incubating young may on occasion fertilize and pick up a new batch of eggs.

slower rate. In most cases, the males gathered up the eggs rapidly and then kept poking around the nest for some time. Thus any scattered eggs were quickly recovered. Some of the females, on the other hand, would pick up part of the eggs, swim away from the nest, return and pick up more eggs, swim away again, and so forth.

The egg-gathering records for the female were necessarily limited by the behavior of the males as noted above. It was therefore considered appropriate to use for comparison data from other experiments. Aronson and Holz-Tucker (unpublished data) observed the spawning of an isolated female that could see another female in an adjacent tank. The ovipositing female took 24′ to start gathering up the eggs and the process itself took 1′25″ to complete. Similarly, we observed the spawning of a completely isolated female. This female did not start to pick up the eggs for 13′5″. She took 1′15″ to gather up most of the spawn, but left six eggs which she did not pick up for another eight minutes. A large number of normal females were paired with males suffering various types of brain lesions (Aronson, in manuscript). In 27 spawnings, these females took on the average 12′2″ to start picking up eggs and an average of 1′15″ to complete the job. Hence these data support our original conclusions. However, it is likely that in our first observations, the mean time for the six females to start picking up the eggs is somewhat low, while the time it took to complete the process may be a little too high. It is of interest to note that in a few spawnings the females seemed unable to carry all of the eggs that they themselves had laid.

Both the male and female are capable of successfully incubating the eggs. The percentage of spawnings in which young were recovered at the termination of the incubatory period is shown in Table II. Where the spawnings were not witnessed, the slightly higher score made by the males may be accounted for by a possible failure to record a few cases where the spawn was swallowed immediately after the oviposition, and before it was observed. The data for the third set of observations are taken from a second experiment, (Aronson, 1945). These spawnings were also not witnessed. In this experiment, aquarium conditions were considerably improved by the use of aquarium filters, thus avoiding any changes of water. The young were forcibly ejected from the parental mouth on or about the tenth day after spawning and were counted immediately, thus largely eliminating the possibility of losses through cannibalism.

Even with these improved techniques, only 40% of the males released viable fry. Two factors account for this low yield of young by the males. First is the failure of the eggs to be properly fertilized, or death of the embryos, with subsequent disintegration of the eggs. A second factor is swallowing the spawn. The relative importance of these two factors will now be considered.

If freshly laid unfertilized eggs are placed in a jar of *Tilapia*-conditioned water which is kept at approximately 26° C., very few of the eggs will show any gross signs of degeneration before 24 hours. Starting with the second day, however, some of the eggs will have decomposed, and in all cases few if any intact eggs remain after the tenth day. As to the variation in the length of the incubation period, it will be seen in columns 6 and 7 of Table III that females may carry unfertilized eggs for as long as ten days, after which time it may be assumed that all have decomposed. Note particularly that in almost 80%[15] of these cases, the dead eggs were retained longer than one day, and it is highly probable that in many of these cases the eggs were carried until they were quite degenerate. It was not unusual to examine the contents of a male's or female's mouth and

[15] Since the presence of incubating eggs was checked only twice daily, spawn swallowed shortly after oviposition might have been overlooked. Hence this figure may be a little too high.

TABLE II.

Per Cent. of Spawnings in which Young Were Recovered.

| | No. of spawnings in which males incubated eggs. | No. of males releasing young. | % of males releasing young. | No. of spawnings in which female incubated eggs. | No. of females releasing young. | % of females releasing young. |
|---|---|---|---|---|---|---|
| Spawnings witnessed. | 68 | 22 | 32.4 | 14 | 3 | 21.4 |
| Spawnings not witnessed. | 85 | 33 | 38.8 | 2 | 0 | 0.0 |
| Spawnings not witnessed, 2nd experiment. | 70 | 28 | 40.0 | 4 | 4 | 100.0 |

## TABLE III.

### Variation in Length of Incubatory Period.

| Length of incubation. | NO YOUNG RECOVERED | | | | | | YOUNG RECOVERED | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Incubated by males[1]. | | Incubated by females[1]. | | Incubated by females[2] (unfertilized eggs). | | Incubated by males[3]. | | Incubated by females[1,4]. | |
| | No. of males. | Per cent. of males. | No. of females. | Per cent. of females | No. of females | Per cent. of females | No. of males. | Per cent. of males. | No. of females. | Per cent. of females. |
| 0- 1 hr. | 1 | 2.2 | 5 | 45.5 | | | | | | |
| 1- 8 hr. | 1 | 2.2 | 1 | 9.1 | 54 | 20.1 | | | | |
| 8-24 hr. | 6 | 13.3 | 0 | 0.0 | | | | | | |
| 2 days. | 7 | 15.6 | 1 | 9.1 | 54 | 20.1 | | | | |
| 3 " | 13 | 28.9 | 1 | 9.1 | 34 | 12.7 | | | | |
| 4 " | 10 | 22.2 | 2 | 18.2 | 44 | 16.4 | | | | |
| 5 " | 1 | 2.2 | 0 | 0.0 | 31 | 11.6 | | | | |
| 6 " | 2 | 4.4 | 1 | 9.1 | 19 | 7.1 | | | | |
| 7 " | 1 | 2.2 | | | 19 | 7.1 | 1 | 1.2 | | |
| 8 " | 0 | 0.0 | | | 6 | 2.2 | 1 | 1.2 | | |
| 9 " | 0 | 0.0 | | | 5 | 1.9 | 1 | 1.2 | | |
| 10 " | 2 | 4.4 | | | 2 | .7 | 2 | 2.5 | | |
| 11 " | 1 | 2.2 | | | | | 12 | 14.1 | | |
| 12 " | | | | | | | 8 | 9.4 | | |
| 13 " | | | | | | | 18 | 21.2 | | |
| 14 " | | | | | | | 12 | 14.1 | | |
| 15 " | | | | | | | 9 | 10.6 | | |
| 16 " | | | | | | | 4 | 4.7 | 1 | 33.3 |
| 17 " | | | | | | | 11 | 12.9 | 1 | 33.3 |
| 18 " | | | | | | | 2 | 2.5 | | |
| 19 " | | | | | | | 1 | 1.2 | 1 | 33.3 |
| 20 " | | | | | | | 3 | 3.5 | | |

[1] All spawnings witnessed.

[2] Females isolated from males. Spawnings not witnessed. Incubation intervals less than 1 day were recorded as one day, but some short intervals might have been missed. Data from Aronson (1945).

[3] Some spawnings not witnessed. Includes data from Aronson (1945).

[4] The young from the four females of the 2nd experiment indicated in Table II were forcibly removed from the parents' mouths on the 12th day. Hence these cases could not be included in this table.

find that the fish had been carrying a mass of badly decomposed eggs, or a mixture of decaying eggs and viable embryos. From the appearance of the eggs it was frequently apparent that the fish had been carrying the dead eggs for many days. In columns 2 and 3 are listed the durations of the incubatory intervals for males carrying fertilized eggs. It will be noted that in 17.7% of the cases, the spawn was swallowed within 24 hours. The indirect evidence cited above leads to to the conclusion that these eggs were swallowed because of some failure of the male's incubatory mechanism, whereby the male failed to discriminate between eggs and food. On the other hand, those egg masses which were retained in the mouth for a number of days were only swallowed when they had become extensively decomposed. It should be noted in passing that decomposed eggs are never found in the tanks, and it is assumed that they are swallowed rather than spat out. The stomach contents of several males were examined shortly after the egg layings, while the males were carrying eggs. In two of these cases a few eggs were also found in the stomachs.

Columns 4 and 5 show that in 54.6% of the spawnings in which eggs are picked up by the females, they were swallowed within 24 hours and in most cases within the first hour after spawning. Although these data are limited, they indicate that the female's incubatory mechanism is not as dependable as the male's, and that the female fails to distinguish eggs from food much more frequently than does the male.

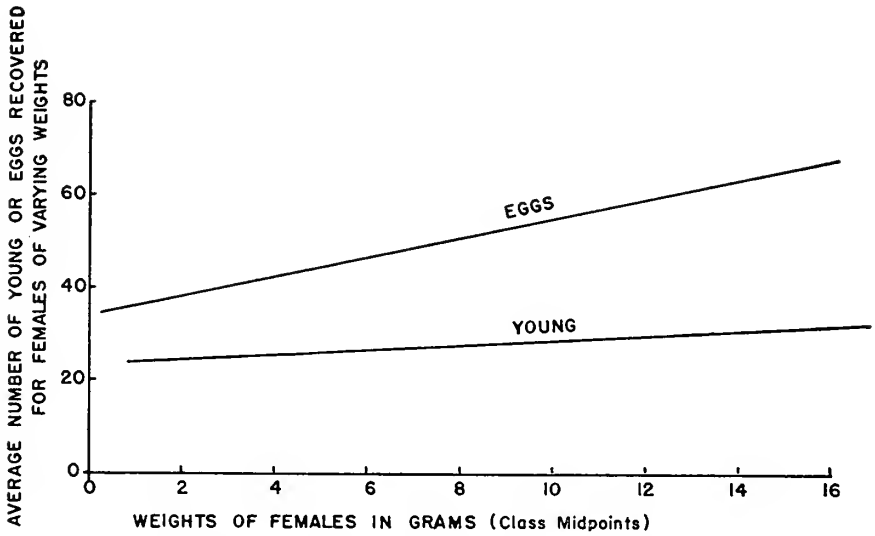
The length of incubation by the male in cases where young are recovered is shown in columns 8 and 9 of Table III. These data fit closely a normal curve, and from them we have determined a mean incubatory time of 13.8 ± .27 days with a standard deviation of ± 2.6 days. This would give us a theoretical range of 6 days to 22 days. The few cases in which the female successfully reared young fall well within this range.

Thus far, only the presence or absence of eggs and developing embryos have been considered. Now, the relative sizes of the spawn and brood will be examined. A new group of pairs was established, and on the day of or day after oviposition, the spawn was ejected from the male's mouth and was counted. This count may be taken to represent fairly accurately the number of eggs laid by the female, since, in most instances, all of the eggs are picked up and few if any are swallowed. Eighty females whose mean weight was 7.15 ± .38 gr. deposited an average of 49.7 ± 1.96 eggs.

In a second group of 31 pairs in which the average weight of the females was only slightly less (5.6 ± .38 gr. ), the males were allowed to incubate the eggs and the fry were counted soon after their release. Here it was found that the average brood size was only 23.9 ± 2.9 young. It was thought at first that this smaller brood size might be attributed to the lesser weights of our second group. To examine this hypothesis the body weights of the females that had just oviposited were compared with number of eggs in the spawn. A low order positive correlation was found, which was probably significant ($r = +.23$ or $z = +.236$; P calculated from $\frac{z}{\sigma z} = .05$). A similar comparison of the weights of females (determined immediately after oviposition) with the size of the brood that was eventually recovered after being incubated by the male partner did not yield a significant correlation ($r = +.10$ or $Z = +.10$; P calculated from $\frac{z}{\sigma z} = .6$). When two regression lines are plotted (calculated by the method of least squares), one for the rise in number of eggs oviposited as body weight increases, and a second for the change in number of young recovered as body weight increases (Text-fig. 10), the relationship involved becomes clearer. From these regression lines in Text-fig. 10, it can readily be seen that for females of the same body weight, the number of young successfully incubated is considerably smaller than the number of eggs laid. This loss can best be accounted for by the failure of some of the eggs to be fertilized and by the death of some of the embryos. Since brooding fish have never been observed to spit out decomposed eggs or embryos, and since such material has rarely been observed on the gravel substrata of the aquaria, it is assumed that the incubating fish somehow manages to sort out and swallow this dead matter.

These data also indicate that while larger females tend to lay a greater quantity of eggs than smaller females, the number of fry successfully brooded by the males remains constant regardless of the weights of the females and hence of the magnitude of the spawn. Therefore the mortality of eggs and embryos must be directly proportional to the size of the female and hence to the number of eggs laid. Since the larger females were in most cases older, this difference might be based upon an aging factor. It is also conceivable that such increased mortality was due to overcrowding in the male's mouth during incubation.

It is an interesting fact that incubating *Tilapia* generally carry some gravel intermingled with eggs. Of 63 fish examined on the day or day after the egg laying, 95.2% were carrying one or more pieces of gravel. Generally between 25 and 50 pieces (commercial grade No. 2) were found along with the eggs, and occasionally the count went well over 100. The possible significance of this fact is not known at present. It is not clear whether or not the gravel is picked up accidently along with the eggs, and whether this behavior bears some relation to the survival of the embryos. For example, it is possible that since the eggs and gravel are continuously churned around in the mouth, the




TEXT-FIG. 10 Regression lines showing relation of body weights of females to number of eggs laid during each spawning and relation of body weights of females that spawned, to number of young recovered immediately after their release by the incubating males.

latter might serve to rub off fungi or ectoparasites from the developing fish.

It is important to note that there is considerable variability in the number of days that given parents may incubate their young. It is therefore to be expected that at the time of release, the broods carried longest will be the ones furthest advanced in development. This, generally speaking, is found to be true. Thus, fry released in less than ten days still have a large yolk sac and their swimming activity is sporadic, whereas young incubated for longer intervals show little or no trace of the yolk sac, also their swimming ability is developed to the stage where they are well able to elude their enemies if reasonable shelter is provided. A complicating factor is that, as can be seen from the few samples in Table IV, there is a considerable difference in the rate at which the fry grow within the parental mouths. Thus the average size of a given brood incubated for 22 days was barely larger than another one incubated only 15 days. Similarly, a given brood retained in the mouth for only 11 days reached the same average size as another brood incubated for 16 days. It is possible the number of young in the brood may somehow be related to growth rate; however, our limited data on this point in Table IV do not suggest such a relationship. It is also of interest to note that the variation within the brood was quite low, the average coefficient of variation (V) for nine broods being 3.7. This state of affairs is in striking contrast to the great variability ($V = 15 \pm 1.60$) which resulted when a brood was kept together in a stock tank from the time of release to maturity (Aronson and Holz-Tucker, in manuscript).

## DISCUSSION.

In most vertebrates the characteristic mating behavior patterns of the two sexes are distinctly different. Thus in the rat, the reproductive habits of which have been analyzed most intensively, the typical pattern of the estrous female, lordosis, is only occasionally exhibited by the male (Beach, 1938, 1945). Similarly, the typical male pattern of ear-wriggling, mounting and pelvic thrusts is seldom seen in the female (Long and Evans, 1922; Hemmingsen, 1933; Beach, 1938).

The sex difference in behavior generally is very clear although relative rather than absolute. Under special conditions males may be induced to exhibit female-like behavior, and the reverse can also be accomplished (Beach, 1941). The conditions producing such results often are very special in nature. Thus for example, the well known fact that estrous cows frequently exhibit male-like mounting behavior may very well result from the almost universal custom of segregating the cows from the bulls. Similarly Beach and Rasquin (1942) explain in part the high incidence of masculine behavior in their female rats as the result of repeatedly testing two females together. These authors are also aware of the possibility that the females of their particular colony may have been more active in a masculine direction than are females from most other stocks. However, we are concerned with the fact that disparity of behavior between sexes is general among the vertebrates.

A survey of the literature indicates that in reptiles a behavioral dichotomy of the sexes appears to be the rule, and the writer's extensive investigations of the sexual be-

TABLE IV.

Relation Between Average Size[1] of Young in Brood and the Number of Days the Brood Was Incubated.

| No. of days young were carried. | No. of fry in brood. | Average length of fry[1] (mm.). | Coefficient of variation. |
|---|---|---|---|
| 10 | 13 | 9.2 ± .08 | 2.9 ± .57[2] |
| 11 | 19 | 10.6 ± .10 | 4.0 ± .65 |
| 11 | 3 | 10.4 | ..... |
| 11 | 8 | 9.8 ± .09 | 2.8 ± .70 |
| 12 | 44 | 10.8 ± .06 | 3.9 ± .41 |
| 14 | 18 | 9.4 ± .11 | 5.1 ± .85 |
| 15 | 82 | 11.2 ± .04 | 3.3 ± .26 |
| 16 | 58 | 10.6 ± .06 | 4.4 ± .40 |
| 16 | 38 | 10.6 ± .06 | 3.7 ± .43 |
| 22 | 58 | 11.5 ± .05 | 3.4 ± .31 |

[1] Length from tip of mouth to end of tail fin.
[2] Standard error of the coefficient of variation.

havior of the tailless amphibia have shown that in the Anura, male and female sexual behavior are quite specific with only occasional evidence of bisexual behavior (Noble and Aronson, 1942; Aronson, 1943, 1943a, 1944).

In many birds these distinctions are less clear. Thus in the pigeon, billing and bowing are common to both sexes (Whitman, 1919), and while it is usual for the female to squat and for the male to mount, copulation not infrequently occurs with the positions reversed (Carpenter, 1933).

While all vertebrates appear to possess the neuromuscular and hormonal mechanisms capable of eliciting most elements of the mating pattern of the opposite sex (Beach, 1942, 1944), morphological differences, particularly in the genitalia, hormones and other genetic factors, greatly limit the incidence, completeness and effectiveness of such behavior. Thus in the majority of vertebrates, behavior patterns characteristic of the male or female are readily distinguished.

In contrast to this typical vertebrate condition, *Tilapia* appears to represent an extreme condition. None of the patterns of reproductive behavior investigated are entirely characteristic of either sex. Qualitatively, male and female courtship and spawning behavior are exactly alike. Even in the acts of oviposition and fertilization, the overt motor patterns are the same in both sexes. Both fish swim slowly over the nest and rub their genital tubes on the substratum. The one observable difference occurs when eggs extrude through the genital aperture of the female, while the male's genital tube releases sperm, which, however, are invisible to the naked eye. It is only when the frequencies of the various reproductive acts are considered that behavioral differences between the sexes become apparent. It is true even so that in *Tilapia* sex differences in behavior depend in some cases on the time interval before the spawning. Thus, as we have found, the females exhibit much more courtship and do most of the nest-building. Males do more nest-passing than the females at one to two hours before the spawning, but at 15 minutes prior to oviposition we find this relationship clearly reversed. After the spawning, both qualitative similarity and quantitative dichotomy are still in evidence. Thus males wait on the average only 1.3′ before they start to pick up eggs; whereas females require on an average 7′59″. Also, males pick up the eggs much faster than the females, and are less prone to swallow their eggs.

In some of the patterns, as for example head-nodding, the quantitative difference between male and female frequency of the act is sufficiently large that such behavior could possibly be called a female pattern. However, our data have shown that in 25 pairs where continuous records for the first hour were available, almost one-third of the males exhibited some head-nodding. It is highly probable that if the entire span of the pre-spawning sex behavior could be observed, an even greater percentage of the males would be found to perform a minimal amount of this behavior. Bisexual or homosexual activity has generally been thought of as a recognizable intrusion of the characteristics of behavior in one sex to a greater or lesser extent into the behavior patterns characteristic of the opposite sex. Such partial observations of sex dichotomy are known to occur in a limited portion of the population or under special circumstances such as segregation. Thus we are justified in considering bisexual or homosexual behavior a rather restricted phenomonon in most vertebrates. It follows that in the case of *Tilapia* none of the patterns should be relegated to one particular sex as is generally done in the higher vertebrates.

One might hypothesize that this situation in *Tilapia* represents a primitive condition in the evolution of reproductive behavior patterns. This, however, is doubtful since cichlids are a highly specialized family of

teleosts, and on the other hand clearly recognizable, sexually divergent mating patterns are in evidence in some of the anatomically more primitive fishes. While our study of the described condition concerns *Tilapia*, it is apparent from the literature that qualitative similarities and quantitative differences such as we find between male and female sexual behavior in this species will be found to a greater or lesser extent in all cichlid fishes, and may well be true of several other families of fish.

Rather than being a primitive condition, we might view these behavior patterns of *Tilapia* as adjustments (in an evolutionary sense) to a specialized mode of reproduction in which the similarity of the sex behavior patterns has a considerable adaptive value. For the post-spawning parental behavior this point is fairly evident. If both sexes are capable of rearing the young, there is less likelihood of lost or wasted spawn. If we look upon the action of courtship as a mutually stimulating and a synchronizing mechanism as well as one which keeps the pair together, one might expect the sexes to develop comparable mechanisms to accomplish the same outcome when not limited by morphological dissimilarities.

Not all behavioral disparities between the sexes in *Tilapia* are readily understandable. On several occasions, males exhibited considerably more courtship activity than the females of given pairs. In no case did such excess lead to a spawning. One observation showed a male in a stock tank courting at a very high frequency as he swam around the enclosure. In the same aquarium a female was engaged in building a nest. Actually she did not court in relation to this sexually active male, but rather her activities had to do with two other males in the territory. The significance of excessive courtship by males is not clear. It is possible that it represents the equivalent of bisexual behavior, that is, of males behaving like females.

In this study we have found it convenient to group certain activities such as the throat-puff, body-quiver, tail-slap and head-nod under the category of courtship, as distinct from subsequent items of the reproductive series, namely nest-building, nest-passing, spawning-quivers, oviposition and fertilization. However, no sharp line of demarcation is implied between these. If we follow the functional definition of courtship as previously stated (page 136), one cannot altogether exclude the latter group of patterns from the courtship category. However, a separation on the basis of functional or adaptive significance seems to be in order. Thus courtship behavior is mainly concerned with the formation and maintenance of the pairs while the latter activities have most to do with the immediate preparation for spawning, as for example the building of the nest and the physiological preparation for oviposition and fertilization. Also there are indications of an organic separation. It is of interest to note in this connection that in our observations on the several days before spawning, most of what we are terming courtship activities were seen at one time or another, but the acts of nest-building, passing-nest and spawning-quivers were never recorded. Thus in general reproductive behavior tends to arise and function in group fashion.

The quantitative records show that all of the courtship responses of the female increased in frequency directly after spawning. The same was true for nipping. Two factors appear to be responsible for this increased activity. The first is a physiological change consequent to oviposition, and the second is the presence of eggs. While we have not attempted to analyze the relative influence of these two factors, several observations are of interest here. First, the observed heightened courtship activity generally lasts several hours and subsides gradually. Secondly, the activity continues long after the eggs have been removed to the male's mouth. The freshly laid eggs might possibly release some type of chemical stimulus, but the evidence for this is not forthcoming. Moreover, if newly oviposited eggs are presented to males and females that have not spawned recently, such eggs are generally eaten within a short time, and they do not stimulate either courtship or nipping. The effect of this heightened activity is not apparent in most of the spawnings, but in the few cases where the males are slow in picking up the eggs, the courting seems to attract the male to the nest and stimulates him to gather up the spawn.

It has long been recognized that certain external morphological characteristics of an animal, together with specific modes of behavior, may act as exciting stimuli to other members of the species (and sometimes to members of another species) for the mediation of specific behavioral responses. Lorenz (1935, 1937) has developed this concept as a cornerstone of his theory of instinctive behavior. The stimulus or group of related stimuli bringing forth a reaction are called "releasers," the responding individual is designated as the "companion." Mutual instinctive responses of companions are sharply separated from learning processes although some modifications of the former are recognized. Furthermore, according to this view the release of every unconditioned reaction is considered to be dependent on a special central nervous mechanism which is called the "innate releasing schema" (Lorenz, 1935) or "innate releasing mechanism" (Tinbergen, 1939, 1948).

These hypotheses have become quite popular on the Continent. In this country they have received some consideration by students of bird behavior, but they are largely out of tune with the findings and interpretations of a large segment of the American experimental psychologists (Lashley, 1938) who in general have paid little attention to the

Lorenz movement. To say that a special "innate releasing mechanism" exists for every unconditioned reaction implies an extreme localization of function within the brain, a claim that is without special support in this country. Here the more popular view is that most responses are capable of being elicited by a broad array of well separated stimuli (Beach, 1942, 1947) and are not exclusively dependent upon any single stimulus or group of stimuli. Moreover, there is here a growing tendency to think of innate and learned factors as closely interlocked in their influence on behavior (Schneirla, 1941, 1946) with the view that in the higher vertebrates at least, purely innate behavior patterns as entities may be simply matters of a convenient terminology doubtfully related to reality. Lack (1940) has criticized Lorenz's view as being too simple. He points out that in many cases the designated releasers may not be the sole characters that bring forth the response. Rand (1941) has been to date Lorenz's severest critic. According to Rand, the releasing characters are by far too limited, and the releasers and responses are mostly unidentified. The reality of releasers has accordingly not been demonstrated but remains presumptive. Actually the experimental analytical approach to behavior is not only untried by Lorenz, but its validity is denied. Finally, according to Rand, there is in Lorenz's treatment a negativistic approach which denies the possibility of ever being able to elucidate the fundamentals of behavior.

Tinbergen (1939) has modified Lorenz's hypotheses in several respects. First, releasers are called "signals" or later "sign stimuli" and are subdivided into releasing stimuli and directing stimuli. More important, Tinbergen recognizes a closer relation than does Lorenz between innate responses released and modifiable factors such as learning, endocrine reactions and neural processes (summation, conditioning and "higher mental processes"). Most important is Tinbergen's recognition of the validity of the experimental approach, and his attempts, mostly by means of artifacts and models, to demonstrate releasers in this manner. Even so, it must be emphasized that Tinbergen sees releasers as very specific and limited morphological and behavioral characters which during the unfolding of a complex pattern of response will hold to a relatively rigid sequence.

Seitz, a follower of Lorenz and Tinbergen, has analyzed the behavior of two related cichlid fishes, namely a small Egyptian mouthbreeder, *Astatotilapia strigigena* (1940) and the jewel fish, *Hemichromis bimaculatus* (1942) in terms of the releaser concept. Seitz recognizes whole series of very specific releasers which call forth specific responses and which lead in an orderly manner to the spawning. These he has summarized in schematic form (1940, p. 82; 1942, p. 100). Thus, in *Astatotilapia*, the presence of a female releases a change to mating coloration in the male, and this change in its turn releases a slight but not significant color change in the female. The presence of the female also releases a mode of behavior called by Seitz an introductory presentation which in turn brings forth a passive response in the female. This in turn releases a complex of movement and color change called by Seitz a "Fegebalz" (lit., sweeping courtship dance). This Fegebalz of the male releases a following reaction on the part of the female, which in its turn releases circular swimming in the male around the spawning site. The circular swimming then releases a strong following reaction of the female to the spawning site which in turn brings forth a response whereby the male slips under the female. This releases circling movements in the female which in turn release the same movements in the male. The circling movements of the male call forth additional circling movements by the female. These release the oviposition movements and the latter release the fertilization movements of the male.

Our experiments were not designed to test the releaser concept and this discussion is not intended as a critique thereof. However, we were interested in learning to what extent our data would or would not support the releaser hypothesis or fit into that pattern of thought.

The significant correlation between male and female nest-passing behavior appeared most likely to fit in with this concept if we were to assume that nest-passing of male and female released a like behavior in the opposite sex. However, we had on record any number of cases where the females were very quiescent, exhibiting little or no courtship or pre-spawning behavior of any kind, and yet the males nest-passed consistently. Of course, the nest itself might be a releaser of nest-passing, but this would contradict a large portion of our data where nest-building by the female and the presence of a well-formed nest was not followed by nest-passing on the part of the male. Similarly in the spawning of the completely isolated female previously referred to, the order of magnitude of nest-passing behavior was well within the range of variability of our control pairs. Yet there was nothing in that situation which could be considered a releaser. In an attempt to follow the lead of Seitz, we could possibly view the various courtship patterns previously described as releasers. For example, the approach-throat-puff of the female might be construed as a releaser of similar behavior by the male which in turn might be thought of as releasing female nest-building behavior. This may be especially so since an approach-throat-puff by a female was often followed by a similar pattern in the male, and soon thereafter the female turned to the construction of the nest. However, no consistent pattern of this type was in evidence. Female throat-puffs were also followed by almost any of the other courtship patterns or by no particular re-

sponses of the male. Again, female nest-building was sometimes preceded by the throat-puffs but often by head-nods, tail-slaps or body-quivers. It is recognized that in general observation, that is in "just watching" these fish, one could easily gain the impression that certain acts are in effect releasers, and others a response to these releasers. However, when observational technique involves an orderly and complete quantification of response according to condition of occurrence, the data do not support such an interpretation.

We are inclined to view the courtship and pre-spawning items of behavior together with the territory and nest as having a general stimulatory effect upon the other member of the pair which would tend to raise the level of sexual excitability in the latter. Or, to put the matter in another way, the given conditions may serve to lower the threshold for the elicitation of various courtship and pre-spawning patterns. Here the particular response obtained would depend upon a whole complex of factors including the neural threshold, the immediate topographic relation to the partner, the territory, the nest and other environmental conditions, as well as the internal physiological balance of the individual at the moment. In this sort of system, no specific releasing stimuli may be properly postulated. For example, a series of weak or only partially effective tail-slaps by the female might bring forth a response in the male similar to one very effective approach-throat-puff. Moreover, as the general level of excitability of both members of the pair increased, there would be a gradual shift in the statistical probability of the elicitation of a given type of response. In other words, throat-puffing during the early stages of the pre-spawning history of a pair might bring forth additional throat-puffing or other phases of the courtship, while later, such behavior might elicit return to the nest or nest-passing. As spawning approached, nest-passing behavior of one member of the pair was often followed by like behavior of the other member of the pair, but this was often interrupted by some of the early phases of courtship such as head-nodding and tail-slapping. In many of the records, interruptions of the smooth flow of passing-nest and spawning-quivers were noted within minutes of the actual oviposition. While these data do not altogether contradict the releaser concept, it is believed that these findings can be more satisfactorily understood by adhering to a considerably more generalized interpretation of the complexity and effectiveness of the stimuli than the "releaser concept" implies.

Seitz (1940) and Tinbergen (1948) in their discussion of releasers refer to the "rule of heterogeneous summation" which states that the release of a given behavior pattern may result from the summation of several different stimuli. Tinbergen also emphasizes that "high internal motivation may cause the reactor to respond to all objects offering the minimum adequate external stimulation." Finally, Tinbergen observes that some releasers have a general excitatory influence, rather than to direct the reactor's response. If these three principles noted here are sufficiently expanded, some of the major objections to the releaser concept are thus overcome, and except for the sharp lines drawn between instinct and learning processes, we begin to arrive at a common ground for the understanding of the nature of sexual behavior.

## Summary and Conclusion.

Qualitative descriptions and quantitative measurements of the patterns of reproductive behavior of the African mouthbreeding cichlid fish, *Tilapia macrocephala* (Bleeker), have been presented. These patterns have been grouped into three categories. The first, namely courtship, includes head-nods, approach-throat-puffs, body-quivers and tail-slaps. Most of the females exhibited these courtship items during the observation periods, and at a relatively high frequency. The males performed these courtship acts at a considerably lower frequency. A high percentage of males showed some tail-slaps and body-quivers, and it is believed that if the entire spans of the pre-spawning activity of the pairs could have been observed, all of the males would have performed these courtship patterns. On the other hand, it appears that a measurable portion of males do not head-nod or approach-throat-puff prior to the spawning.

It is hypothesized that courtship behavior is an expression of the level of excitability of the individual. It may be thought of as a trophallactic process which through mutual stimulation serves to regulate the behavioral activities and physiological processes of the male and female so that well synchronized spawnings result.

Nipping, which is closely related to courtship and which also appears to be mutually stimulating, was performed equally by the male and female before the spawning, but nipping on the part of the female rises sharply directly after oviposition. Similar post-spawning increases on the part of the female were noted for all of the courtship patterns. It is suggested that the physiological changes following oviposition plus the presence of eggs are the factors responsible for this heightened activity. During the inter-spawning interval, a low level of courtship is in evidence, especially on the part of the females.

The second group of reproductive patterns includes those acts which are concerned with the immediate preparation for spawning. Included here are nest-building, nest-passing, spawning-quivers, oviposition movements and the act of fertilization. Considerably more nest-building is exhibited by the

female than by the male, but it is likely that all males do some nest-building before every spawning. With passing-nest and spawning-quivers the frequency is somewhat higher for the males an hour or so before spawning, but at 15 minutes before spawning this relationship is clearly reversed, with the females at the height of their nest-passing and spawning-quivers. A significant correlation between male and female nest-passing during the first pre-spawning interval suggests that this behavior is mutually stimulating. The mean number of oviposition movements of the female did not differ significantly from the mean number of fertilization acts of the male. Moreover these behavior patterns are highly correlated, suggesting that the number of times the male fertilizes the eggs is partly related to and probably dependent upon the number of oviposition movements of the female. In contrast with the courtship patterns, behavioral items in the present category were not observed during the inter-spawning interval.

The third category of reproductive acts are those associated with the care of eggs and young. Males start picking up eggs on an average of 1'3" from the beginning of oviposition. Females, if given the opportunity, took on the average 7'59". This is the apportioning mechanism whereby males usually incubate the eggs, and females do so only on infrequent or special occasions. Similar quantitative differences were found in other phases of the parental pattern. Thus females gather up the spawn more slowly and are more prone to swallow the eggs.

A low order positive correlation was found between the size of the female and the number of eggs laid during a given spawning. Since brood size shows no correlation with the size of the female, it is concluded that a greater mortality occurs in the larger broods. Incubating fish generally carry some gravel intermingled with the spawn, but it was not clear whether this bore any relation to the survival of the embryos.

In the majority of vertebrates there are distinct qualitative differences between the patterns of reproductive behavior of the male and female. While both sexes have the neuromuscular mechanism capable of eliciting both the male and female patterns, bisexual or homosexual behavior is limited and generally appears under special conditions. *Tilapia* are exceptional in this respect insofar as there are no distinct qualitative differences between male and female in their sexual activities. However, there are marked quantitative differences in all of the patterns.

Several previous investigators have analyzed cichlid mating behavior in terms of Lorenz's releaser concept. It is felt that even in the expanded and modified form presented by Tinbergen, this concept is still too restricted to form an adequate basis for the analysis of *Tilapia* reproductive behavior.

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## EXPLANATION OF THE PLATES.

### PLATE I.

Fig. 1. Male cleaning nest. × .5

Fig. 2. Oviposition. The male is behind the female, waiting for her to move along so that he can pass over and fertilize the eggs. × .5

### PLATE II.

Fig. 3. The male is fertilizing the eggs while the female is circling the nest. By the time fertilization was completed the female was directly behind the male, ready to lay a second round of eggs. × .5

Fig. 4. Male picking up the eggs. All of the eggs were gathered up in less than one minute. × .5

### PLATE III.

Fig. 5. Male carrying eggs. × .7
(Photo. by S. C. Dunton, N. Y. Zool. Soc.).

Fig. 6. In special circumstances the female may carry the spawn. An egg can be seen at the tip of the open mouth of the female. × .5

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### ADDENDUM.

When this report was in page proof an article by Alfred Seitz (1948)—Vergleichende Verhaltensstudien an Buntbarschen (Cichlidae).—Zeitschrift für Tierpsychologie, *6* (22): 202-235, was received from Germany. Here Seitz analyzes fighting and courtship behavior in two cichlid species, *Tilapia heudeloti* and *Tilapia natalensis*, in accordance with the theory of instinctive movements of Konrad Lorenz. On page 134 of the present paper we have noted the very close similarities of *T. heudeloti* and *T. macrocephala;* they may in fact be varieties or subspecies. However, the pictures of *T. heudeloti* presented by Seitz, the descriptions of the external morphology, particularly coloration, as well as the descriptions of courtship and fighting behavior, all suggest that he was dealing with a very different fish. It is not possible at this time to comment further on Seitz's paper, nor do we wish to venture any opinions concerning the complex problems of cichlid taxonomy, except to suggest to the reader who may wish to compare Seitz's paper with the present report that the *T. heudeloti* of Seitz and our *T. macrocephala* are perhaps very different species. —L.R.A.

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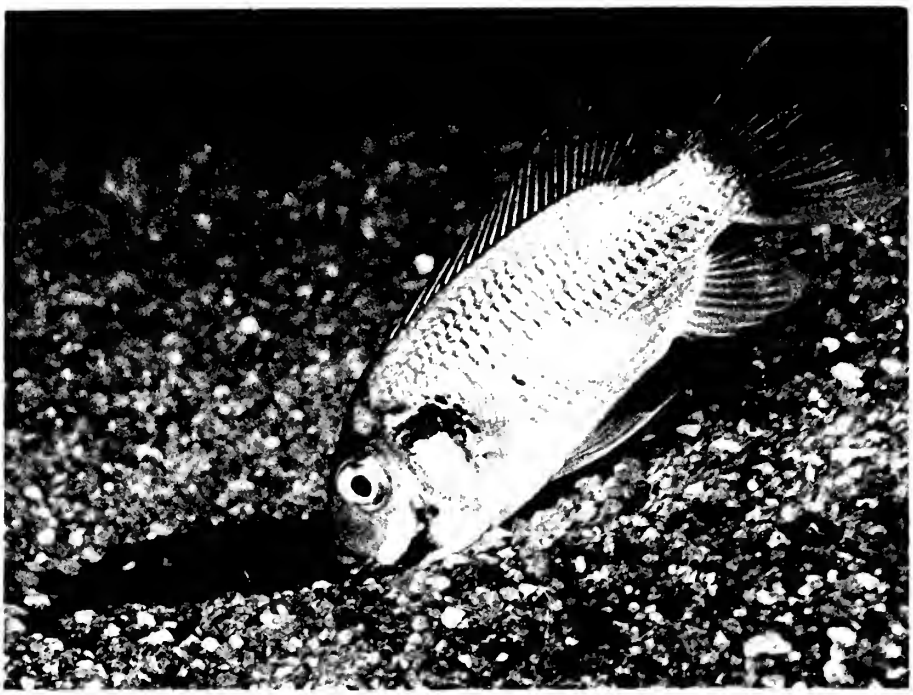

FIG. 1.

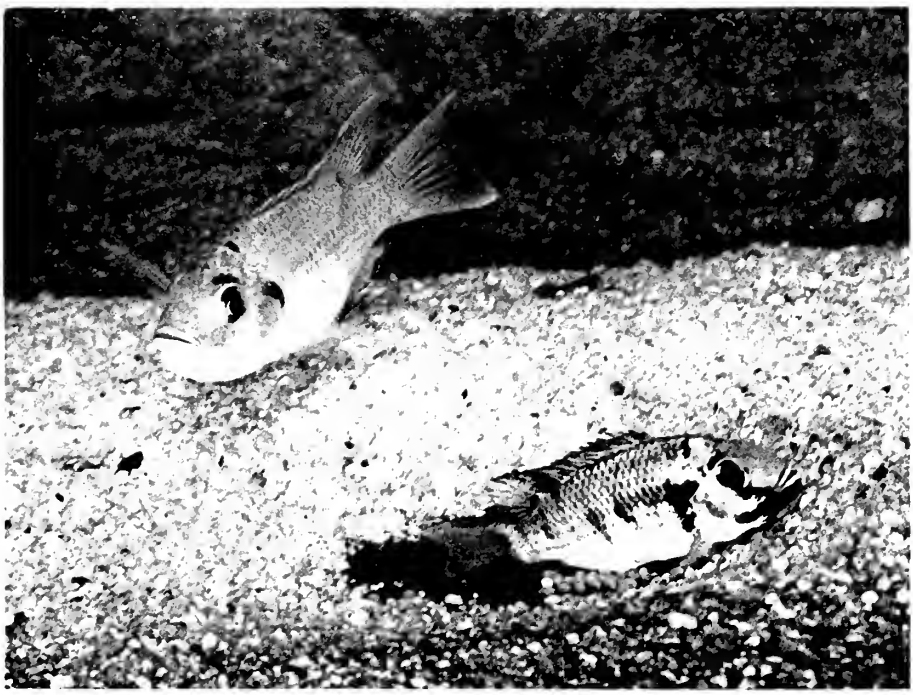

FIG. 2.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

FIG. 3.

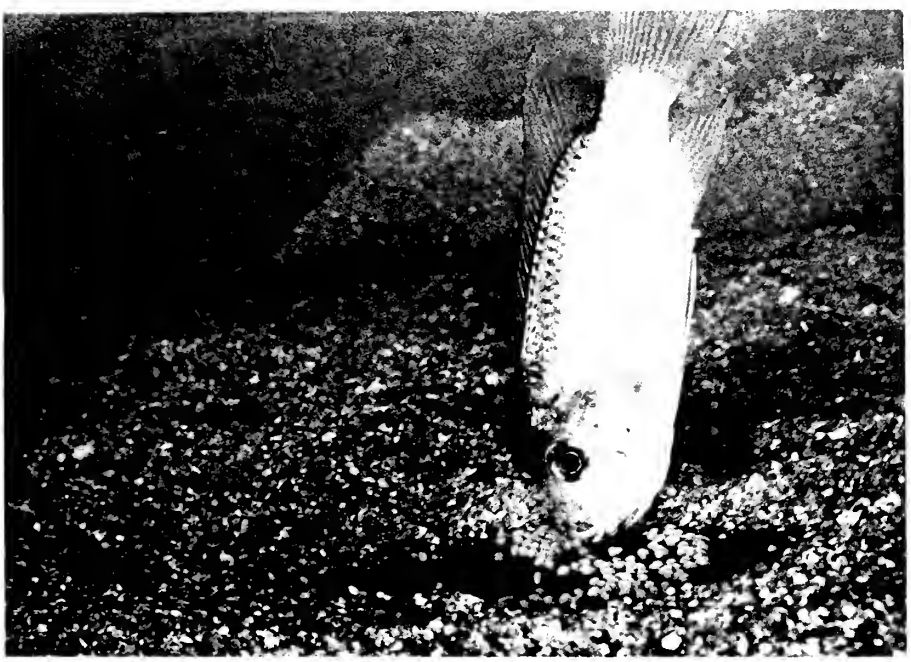

FIG. 4.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

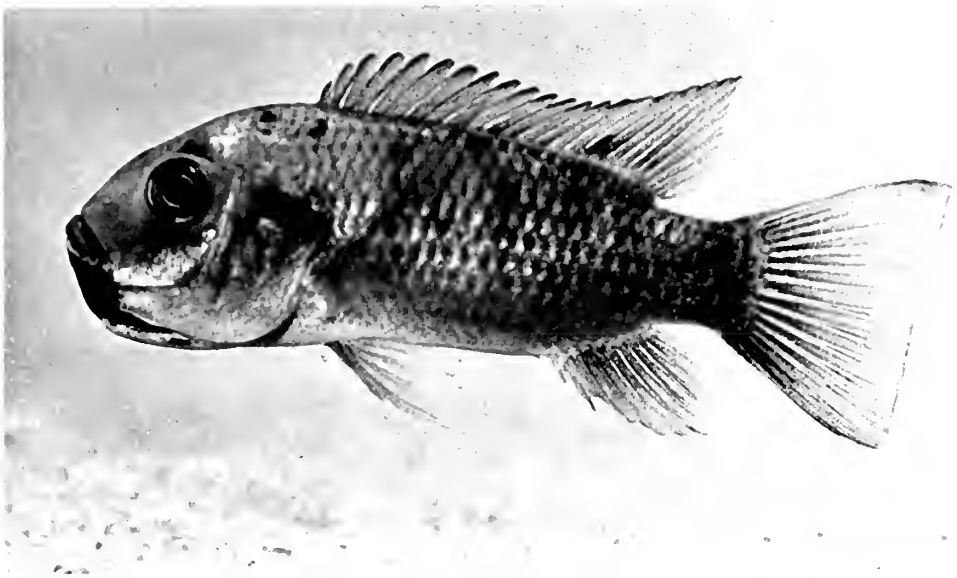

FIG. 5.

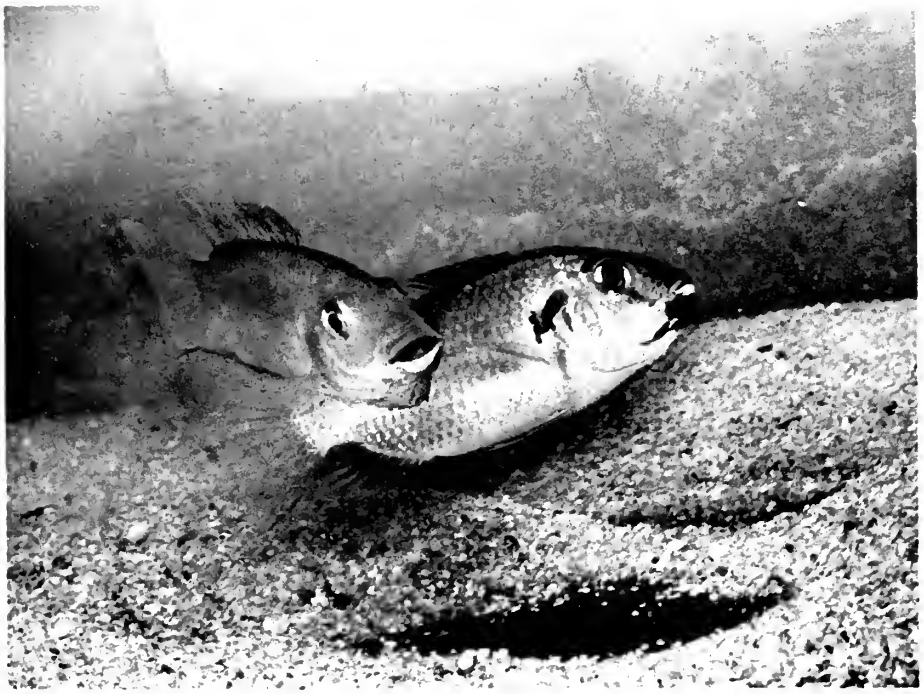

FIG. 6.

AN ANALYSIS OF THE REPRODUCTIVE BEHAVIOR OF THE MOUTHBREEDING CICHLID FISH, TILAPIA MACROCEPHALA (BLEEKER).

# 17.

# Comparative Biology of Salticid Spiders at Rancho Grande, Venezuela. Part IV. An Analysis of Display.[1]

JOCELYN CRANE.

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(Plate I; Text-figures 1-9).

[This is one of a series of papers resulting from the 45th, 46th and 47th Expeditions of the Department of Tropical Research of the New York Zoological Society, made during 1945, 1946 and 1948 under the direction of Dr. William Beebe, with headquarters at Rancho Grande in the National Park of Aragua, Venezuela. The expeditions were made possible through the generous cooperation of the National Government of Venezuela and of the Creole Petroleum Corporation.

[The characteristics of the research area are in brief as follows: Rancho Grande is located in north-central Venezuela (10° 21′ N. Lat., 67° 41′ W. Long.), 80 kilometers west of Caracas, at an elevation of 1,100 meters in the undisturbed montane rain forest which covers this part of the Caribbean range of the Andes. Adjacent ecological zones include seasonal forest, savanna, thorn woodland, cactus scrub, the fresh-water lake of Valencia and various marine littoral zones. The Rancho Grande area is generally subtropical, being uniformly cool and damp throughout the year because of the prevalence of the mountain cloud cap. The dry season extends from January into April. The average humidity during the expeditions, including parts of both dry and wet seasons, was 92.4%; the average temperature during the same period was 18° C.; the average annual rainfall over a five-year period was 174 cm. The flora is marked by an abundance of mosses, ferns and epiphytes of many kinds, as well as a few gigantic trees. For further details, see Beebe and Crane, *Zoologica*, Vol. 32, No. 5, 1947. Unless otherwise stated, the specimens discussed in the present paper were taken in the montane cloud forest zone, within a radius of one kilometer of Rancho Grande.]

## CONTENTS.



## I. INTRODUCTION.

This is the fourth of a series of papers dealing with the salticid spiders of Rancho Grande, Venezuela. Part I (Crane, 1948.1) discussed the taxonomy and life histories of three species of *Corythalia*, Part II (1948.2) described methods of study and Part III (1949) dealt with systematics and behavior in eight new species of various groups of genera, as a basis for this and subsequent sections. The present paper on display, while an independent unit, will be followed by sections on comparative post-embryological development and on evolutionary trends, which must, to some extent, be anticipated in the present paper.

My deep appreciation goes to Dr. William Beebe for his continued advice, encouragement and patience during the progress of this study. Special thanks are due Miss

[1] Contribution No. 858, Department of Tropical Research, New York Zoological Society.

This paper was awarded Honorable Mention in the A. Cressy Morrison Prize Competition of the New York Academy of Sciences for 1949.

Louise A. Moore and Mr. Douglas G. Boyden for their work on the drawings and diagrams, respectively.

## II. PURPOSE.

The purpose of this paper is two-fold: first, to analyze the innate releasing mechanism of display behavior in salticids; second, through a comparison of display and related behavior in widely scattered genera, to shed light on evolutionary trends within the family.

## III. MATERIAL AND METHODS.

The observational and experimental material in this paper has been drawn primarily from about fifteen species of salticid spiders which are common around Rancho Grande, Venezuela. They were carefully selected from among some thirty-five species in the same locality, in which display behavior was to some degree observed, on the following bases:

1. They represent a wide divergence of salticid forms, belonging to seven relatively well-defined groups of genera. These groups, although they have so far defied satisfactory divisions in keys to include all their borderline genera, are still rather generally recognized as composed of naturally related forms. For convenience, Petrunkevitch's (1928, 1939) practice of terming the groups "subfamilies" is followed, although their unequal values and the usual difficulties of salticid systematics are fully recognized. Since the tracing of a pattern of relationships is one of the purposes of this paper, groupings must be attempted. The genera chosen are relatively non-controversial, as are, in their broad outlines, the subfamilies to which they are referred; borderline cases have purposely been omitted. The selected forms are fairly typical members of the following subfamilies designated by Petrunkevitch: Marpissinae, Synagelinae, Dendryphantinae, Magoninae, Hyllinae and Plexippinae. The *Lyssomanes* group, however, in spite of its aberrant characters will be given only subfamilial status. These terms will be used throughout, in order to simplify correlation by future workers, in spite of questionable validity or priority in any of the old, type genera. Each subfamily corresponds to a group in Chickering's 1946 arrangement, based on Panamanian genera, except that in the present paper the plexippinids and hyllinids will be kept separate, largely in deference to basic behavior differences. From these limitations, it will be seen that the study cannot be expected to help in practical fashion in the determination of fine points of relationship among puzzling genera; rather, it is hoped only to clarify some of the broad outlines of the family's organization.

2. The second criterion of selection has been that each subfamily have a northern as well as neotropical distribution. This has a double advantage, since some comparable display behavior has in each case been already recorded and future comparisons will be facilitated.

3. In three genera, *Sassacus*, *Phiale* and *Corythalia*, intrageneric behavior patterns could be compared.

The thirteen species listed in Table I form the paper's foundation, in the sense that most of the observations and experiments were performed on them. Ten of them were described as new in Parts I and III of this study (1948.1, 1949); the remaining three are well known in the tropics. For further comparison, a few casual references will be made to the following Rancho Grande species which are systematically undetermined: Magoninae: *Hypaeus* sp., Dep't. of Tropical Research Cat. No. 45138; Hyllinae: *Phiale* sp., Cat. No. 481408; Plexippinae: *Eustiromastix* sp., Cat. No. 45110; Plexippinae: a genus, probably new, near *Capidava*, Cat. No. 4586.

In Table II an effort has been made to correlate the relevant observations made upon northern species of the same subfamilies by previous investigators. Complete spider display references to 1939 are given in Bonnet's bibliography (1945, p. 718). Kaston (1936) and Bristowe (1941) give excellent selected references on the subject.

The general methods of observation and experiment at Rancho Grande have already been recorded (Part II, 1948.2). Special information regarding particular experiments will be presented in the body of this paper. See also Pl. I, Fig. 2.

It remains to remark on the usage of several terms. The phrase "epigamic display" has been advocated by a number of behaviorists to replace "courtship," a word which has an undesirable historical burden of anthropomorphism. In the study of salticids, the choice is complicated by the wide range of distinctness of male-female, female-male and inter-male display; a general term seems necessary to cover the entire field. Again, "aposematic display" has been proposed to designate inter-male encounters; in the literature, however, this term is used so widely to cover displays against potential predators—a type of display which is not known to occur in salticids—that a more restricted name appears desirable. Therefore, for present purposes, the following terminology has been adopted: *Epigamic display* refers to special behavior of either sex which is normally used in any sexual situation, including encounters between males. *Courtship* applies to those forms of epigamic display which normally precede copulation. *Threat display* is used for all inter-male display, whether or not it is visually distinct from courtship, and whether or not occasional contact fighting occurs.

"Ornamentation" is used as a convenient term to cover special colors, patterns, tufts, brushes, etc., which, conspicuous to human eyes, are specializations possibly connected

TABLE I.

| Subfamily acc. to Petrunkevitch (1939) | Group acc. to Chickering (1946) | Name |
|---|---|---|
| Lyssomaninae | Lyssomaninae | *Lyssomanes bradyspilus* Crane, 1949 |
| Marpissinae | *Marpissa* Group | *Menemerus bivittatus* (Dufour, 1831) |
| Synagelinae | *Zuniga* Group | *Semorina brachychelyne* Crane, 1949 |
| Dendryphantinae | *Metaphidippus* Group | *Ashtabula furcillata* Crane, 1949 |
| Dendryphantinae | *Metaphidippus* Group | *Sassacus flavicinctus* Crane, 1949 |
| Dendryphantinae | *Metaphidippus* Group | *Sassacus ocellatus* Crane, 1949 |
| Magoninae | *Amycus* Group | *Mago dentichelis* Crane, 1949 |
| Hyllinae | *Phiale* Group | *Phiale dybowskii* (Taczanowski, 1871) |
| Hyllinae | *Phiale* Group | *Phiale flammea* Crane, 1949 |
| Plexippinae | *Phiale* Group | *Plexippus paykullii* (Audouin, 1827) |
| Plexippinae | *Phiale* Group | *Corythalia chalcea* Crane, 1948.1 |
| Plexippinae | *Phiale* Group | *Corythalia fulgipedia* Crane, 1948.1 |
| Plexippinae | *Phiale* Group | *Corythalia xanthopa* Crane, 1948.1 |

with epigamic displays. It and similar words are put in quotation marks when it seems wise to emphasize their non-anthropomorphic use. The quotations will simultaneously act as reminders, as advocated by Korzybski (1948), of the every-day, inexact connotations of the terms; another of his safety devices, the frequent use of *etc.*, is employed, not to disguise ignorance, but to emphasize the incomplete state of our knowledge.

The terms *sign stimulus, releaser, director, innate releasing mechanism, stimulus configuration* and *heterogeneous summation* are used with the meanings attached to them in Tinbergen's general discussion, in English, of social releasers (1948).

Throughout the present paper, the terms *reaction* and *response* are used interchangeably to indicate overt display behavior discernible to the human observer.

Kaston's (1948) nomenclature is followed in all references to species of salticids occurring in the United States.

## IV. SURVEY OF SALTICID DISPLAY.

### A. Form and Variety.

The general habits and life histories of all salticids are similar and typical of many hunting spiders; they spin no snares, but stalk and leap upon their prey, which they eat promptly; the male copulates in the dorsal position; the female guards the egg cocoon until the emergence of the spiderlings. In the development of their eyes, however, salticids are unique even among long-sighted hunting spiders. In company with the latter, notably the lycosids, and correlated with the acute vision, the salticids have evolved a courtship display which is primarily visual. This is in contrast to the behavior of short-sighted forms, such as the web-spinning epeirids, in which courtship depends on senses other than vision.

As in all groups, there is considerable intra-family variation in details of behavior, particularly in the form and care of the cocoons, in jumping methods, in preferred ecological niches and in physiological tolerances of various kinds. A most important series of differences is based upon an apparently unreported correlation between visual acuity and chemical dependence on the one hand, and method of locomotion on the other. Because of its basic connection with display behavior, this subject will be considered in detail further on (p. 173).

The outstanding directions of development within the family are shown in the very remarkable variety of epigamic display patterns and in the apparently correlated ornamentation of the spiders. All salticids, before inserting the sperm-charged palps into the epigynum of the female, perform some sort of preliminary motions, the form of which, under natural conditions, is a fixed part of the behavior pattern for the species. These movements range from brief and simple elevations of the first legs to complicated and prolonged sequences involving most of the other appendages.

In some salticids there are clear visual distinctions between courtship and intermale threat display, which often employ not only distinctive motions but also different appendages. In each kind of epigamic display, when complete, there are always distinguishable two major stages. Specific display differences, as well as distinctions between courtship and threat, always lie principally in Stage I. Stage II, which immediately precedes either copulation or true fighting as the case may be, is very similar throughout the family; it consists in extending the first legs forward, parallel to each other and slightly elevated. (Pl. I, Fig. 1).

Although salticid display is dominantly visual, the role of other senses is proving of considerable secondary importance. Unfortunately, because of the limitations of human sense organs and the lack of appropriate instruments, specific display descriptions must still be largely confined to the reporting of gross visual components. For instance, possible changes in chemical stimuli, which may be emitted in sequence during display, are still necessarily overlooked.

Table II presents correlated data on the displays recorded within the subfamilies

## TABLE II.

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Name | Display References | Courtship Posture (Stage I) |
|---|---|---|
| | MARPISSINAE | |
| *Marpissa undata* (De Geer) | Peckham, '89, p. 43; fig. (*"Marptusa familiaris"*) (U.S.A.) | Carapace high. 1st & 2nd legs raised slightl stretched laterally. Abdomen pendent. |
| *Marpissa rumpfi* Scop. | Bristowe, '29, p. 330 352. Bristowe, '41, p. 480; fig. (England) | Carapace high. 1st legs raised vertically, parallel. Abdomen raised. |
| *Menemerus bivittatus* (Dufour) | Crane (Unpublished observations) (Venezuela) | Carapace low. 1st legs raised slightly, stretche antero-laterally; 2nd legs e tended forward. Abdomen level. |
| *Hyctia nivoyi* Luc. | Berland, '27, p. 15; fig. Bristowe, '29, p. 329; fig. Bristowe, '41, p. 484; fig. (Europe) | 1st legs stretched forward @ ∠ 45°; raised & lowered. Abdomen often bent sideways. (c Dendryphantinae). |
| *Hyctia pikei* Peckham | Kaston, '48, p. 455; fig. (U.S.A.) | Carapace low. 1st legs raised vertically @ ∠ 45°. 2nd legs extended forward. Abdomen raised. |
| *Salticus cingulatus* Panz. | Bristowe, '29, p. 332. (England) | Similar to *S. scenicus*. |
| *Salticus scenicus* (Linn.) | Peckham, '89, p. 39. (*"Epiblemum scenicum"*) Gerhardt, '21, p. 131. (*"Epiblemum scenicum"*) Monterosso, '24, p. 1. Bristowe, '29, p. 332. Bristowe, '41, p. 480, 499; fig. (Europe & U.S.A.) | 1st legs slightly raised, stretche laterally. Chelicerae opened. Palps stretched laterally. |
| | SYNAGELINAE | |
| *Synageles venator* Luc. | Bristowe, '41, p. 485. (England) | 1st legs stretched forward, parallel Abdomen wriggled or waved from side to side, sometimes raised a little. |
| *Semorina brachychelyne* Crane | Crane, '49, p. 37. (Venezuela) | 1st legs stretched forward, @ 90° ∠, slightly raised. Abdomen raised; tends to remain high with increasing excitement. |
| *Gertschia noxiosa* (Hentz) | Kaston, '48, p. 451; fig. (U.S.A.) | 1st legs braced laterally. Abdomen raised vertically & swung from side to side. |
| *Peckhamia picata* (Hentz) | Peckham, '89, p. 43. Peckham, '90, p. 121; fig. (U.S.A.) | Carapace high. 1st legs on ground, bent, convex surface forward. Abdomen raised vertically. Spider sways from side to side. |

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| ıreat Posture & Fighting | Principal Apparent Morphological Adaptations to Display | Locomotion & Remarks |
|---|---|---|
| | MARPISSINAE (cont.) | |
| | Slight enlargement basal half of 1st & 2nd legs. | ♀ vibrates palps. |
| aws opened; pressed against those of opponent. | 1st legs elongated, enlarged, darkened. | |
| Jusually ♂♂ pay no attention to each other; no distinctive motions; rarely courtship to mirror image in closed vial. | 1st legs elongated, enlarged, darkened. | Runs; jumps only on prey or to cross gaps.<br>1st legs little used in walking.<br>♀ vibrates pale palps. |
| | 1st legs elongated, enlarged, darkened. | |
| | 1st legs elongated, enlarged, darkened.<br>Abdomen boldly striped. | 1st legs not used in walking, extended forward & raised to clear ground. |
| | Chelicerae elongated, enlarged, darkened.<br>1st legs slightly elongated. | |
| ıike courtship, but jaws opened wider and palps not stretched to sides.<br>No mirror display. Crane obs. U.S.A.) | Chelicerae elongated, enlarged, darkened.<br>1st legs slightly elongated. | Jerky walk; hops when pursued. (Crane obs. U.S.A.). |
| | SYNAGELINAE (cont.) | |
| | 1st legs enlarged. | |
| ıpparently no inter-male display. No mirror display. | 1st legs elongated, enlarged, darkened.<br>Abdomen dark with 2 dorsal white spots. | Runs; jumps only on prey or to cross gaps.<br>1st legs stretched to front, parallel; do not touch ground.<br>♀ vibrates palps. |
| | 1st legs elongated, enlarged, darkened.<br>Abdomen dark with dorsal white bands. | Runs slowly, irregularly, like ant.<br>(Emerton, 1909). |
| | 1st legs elongated, enlarged, darkened.<br>Abdomen dark with dorsal white bands. | |

TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Name | Display References | Courtship Posture (Stage I) |
|---|---|---|
| | LYSSOMANINAE | |
| *Lyssomanes bradyspilus* Crane | Crane, '49, p. 34; see also Text-fig. 8, this paper. (Venezuela) | Carapace high, occasionally bobbe<br>No legs raised; 1st 3 prs. brac forward.<br>Palps sometimes tap ground.<br>Abdomen pendent, twitched.<br>Prolonged posing in this positio as—<br>Rate of retinal motions within AM are accelerated. |
| | DENDRYPHANTINAE | |
| *Ashtabula furcillata* Crane | Crane, '49, p. 41; fig. (Venezuela) | Carapace high.<br>1st legs stretched laterally, wave up & down.<br>Palps jerk; later are quiet.<br>Abdomen turned to side. |
| *Hentzia mitrata* (Hentz) | Peckham, '89, p. 49; fig. ("*Icius mitratus*") (U.S.A.) | Carapace high.<br>1st legs stretched laterally, held a right ∠ to body.<br>Abdomen twisted to side. |
| *Icius elegans* (Hentz) | Peckham, 89, p. 46. ("*Dendryphantes elegans*") (U.S.A.) | 1st legs waved "in way that remind one of a wind-mill". Later, re volves on tip-toe. |
| *Sassacus ocellatus* Crane | Crane, '49, p. 45. (Venezuela) | Carapace scarcely elevated.<br>1st legs stretched up & out at righ ∠ to each other.<br>Chelicerae closed.<br>Palps vibrated occasionally.<br>Abdomen sometimes twisted slightl to side, held motionless. |
| *Sassacus flavicinctus* Crane | Crane, '49, p. 41. (Venezuela) | Carapace moderately high.<br>1st legs stretched up at wide ∠ t each other.<br>Chelicerae stretched sideways, bu closed.<br>Palps stretched sideways.<br>Abdomen trailed inconspicuously from side to side.<br>Later: Carapace & abdomen slowly rocked from side to side. |
| *Metaphidippus protervus* (Walck.) and/or *M. galathea* (Walck.) | Peckham, '89, p. 45; fig. ("*Dendryphantes capitatus*") (U.S.A.) | Carapace low.<br>1st legs stretched forward, close to ground, slightly curved with tips turned up.<br>Palps given circular movement.<br>Later, lies on side, legs still extended. |
| *Paraphidippus marginatus* (Walck.) | Peckham, '89, p. 50; fig. ("*Philaeus militaris*") (U.S.A.) | 1st legs raised, curved toward each other, tips nearly meeting.<br>Palps moved up and down. |

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Threat Posture & Fighting | Principal Apparent Morphological Adaptations to Display | Locomotion & Remarks |
|---|---|---|
| | LYSSOMANINAE (cont.) | |
| Threat display rarely induced; posture as in courtship, but no bobbing, no abdominal twitching, no acceleration of retinal motions.<br>Fighting & mirror display absent. | Distal portion of black retina contrasts with green surroundings.<br>Chelicerae elongated but not specially displayed. | Runs in short spurts. Jumps only in final pounce on prey.<br>Palps pendent, pat ground during pauses.<br>1st legs take part in locomotion.<br>♀ sags to side when watching display; muscular activity in eyes increase as in ♂. |
| | DENDRYPHANTINAE (cont.) | |
| Apparently no inter-male display. No mirror display. | 1st legs elongated, enlarged, darkened, fringed.<br>Abdomen with lateral white stripe bounded by iridescence. | Runs; jumps only on prey or to cross gaps.<br>1st legs unused in progress, held forward, they & palps tap ground; waved in air in pauses.<br>♀ vibrates palps. |
| Same as courtship.<br>Chases rivals away. | 1st legs elongated, fringed.<br>Abdomen with lateral white stripe bounded by darker. | ♀ "indifferent"; sometimes attacks ♂. |
| | Carapace with frontal tufts.<br>1st legs elongated; tibia fringed, black-spotted.<br>Both sexes covered with iridescent scales. | ♀ irritable, prone to attack; later raises abdomen or turns it sideways. |
| Stage I: Similar to courtship, except chelicerae partly unsheathed, & no distinct abdominal twisting.<br>Stage II: Actual fighting, 1st legs raised vertically; chelicerae wide open; palps extended laterally. Clinching frequent, with occasional injury; no deaths seen. | 1st legs elongated, enlarged, darkened, with white scales.<br>Chelicerae elongate, enlarged darkened.<br>Clypeus with white band.<br>Abdomen with large, subdistal, white-barred black spots. | Runs; jumps only to catch prey & cross gaps.<br>1st legs held forward, scarcely touch ground; these & palps wave in air & tap ground, during pauses.<br>♀ once did weak mutual display. |
| Stage I: Like courtship except no rocking.<br>Stage II: (Rare). Chelicerae unsheathed, extended forward; 1st legs raised vertically; clinching; no injuries seen.<br>Occasional mirror display. | 1st legs elongated, enlarged, darkened.<br>Chelicerae elongate, enlarged, darkened.<br>Clypeus with yellow band. | Runs; jumps occasionally when pursued, as well as to catch prey & cross gaps.<br>Palpates ground & waves 1st legs less than *S. ocellatus*. |
| Distinct from courtship. 1st legs raised. Sparring, chasing & clinching without injury. | 1st legs elongated, enlarged.<br>White markings on dark palps & clypeus. | Runs, but hops freely when pursued, as well as to catch prey to cross gaps.<br>Palps often jerk.<br>1st legs not waved. Take some part in walking.<br>(Crane obs. U.S.A.) |
| Distinct from courtship.<br>1st legs raised.<br>Palps vibrated.<br>Abdomen dragged to either side.<br>Chasing and clinching without injury. | 1st legs elongated, enlarged.<br>Chelicerae elongated. | ♂♂ guard immature ♀♀ until molt. |

TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Name | Display References | Courtship Posture (Stage I) |
|---|---|---|
| | DENDRYPHANTINAE (cont.) | |
| *Phidippus audax* (Hentz) | Peckham, '89, p. 45. ("*Phidippus morsitans*") Kaston, '36, p. 120; fig. (U.S.A.) | Carapace moderately high. 1st legs raised in 2 jerks, stretched obliquely out at ∠ of 45° to ground; later waved alternately. Palps raised and lowered rapidly when close to ♀. |
| *Phidippus clarus* Keyserling | Kaston, '36, p. 118; fig. (U.S.A.) | Carapace moderately high. 1st legs stretched out, the femur obliquely up, other segments paralleling ground. Palps sometimes widely spread. Abdomen now & then moved from side to side. |
| *Phidippus purpuratus* Keyserling | Kaston, '36, p. 121; fig. (U.S.A.) | Carapace high. 1st legs stretched out, held higher than in *clarus* & *audax*; waved. Palps held wide apart, parallel with each other, occasionally drummed on ground. Abdomen dropped. |
| *Phidippus whitmanii* Peckham | Peckham, '89, p. 44. ("*Phidippus rufus*") (U.S.A.) | Carapace high. 1st legs stretched forward & up, crossed at tips. Palps held wide apart, parallel with 2nd legs. Abdomen dropped. Sways during advance. |
| | HYLLINAE | |
| *Evarcha falcata* Bl. | Bristowe, '29, p. 333. Bristowe, '41, p. 480. (England) Homann, '28, p. 249; fig. ("*E. blanchardi*") (Germany) | Some waving of 1st legs & twitching of abdomen, but tends to leap on ♀ with almost no display. |
| *Philaeus chrysops* Poda | Berland, '14, p. 116. Thomas, '29, p. 267. Bonnet, '33, p. 139; fig. (France) | Carapace high. 1st legs raised & waved up & down. Palps vibrated. Abdomen slightly elevated. Courtship sometimes almost absent. Leaps on ♀ suddenly. |
| *Phiale flammea* Crane | Crane, '49, p. 48. (Venezuela) | Carapace high. 1st legs raised at 45° ∠ to each other & ground. Palps vibrated irregularly. Abdomen lowered. Carapace rocked from side to side. Later, sinks low, 1st legs stretched to front. |

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Threat Posture & Fighting | Principal Apparent Morphological Adaptations to Display | Locomotion & Remarks |
|---|---|---|
| | DENDRYPHANTINAE (cont.) | |
| Like courtship, until opponents close; then chelicerae & fangs opened wide; some ♀ fighting. | 1st legs elongated, enlarged, with white fringes and scales. Palps with white scales. | Both sexes savage, prone to eat mate. |
| As in *P. audax*. | 1st legs elongated, enlarged, lightly fringed. Palps with white band. | |
| | 1st legs elongated, enlarged, heavily fringed. Clypeus with white fringe. | |
| | 1st legs elongated, enlarged, heavily fringed. | Hopping well developed. |
| | HYLLINAE (cont.) | |
| | 1st legs elongated, enlarged, darkened; palps pale, white-haired. | |
| | 1st legs elongated, darkened with light tufts & scales. | Excellent visual acuity; hops skilfully when pursued. Berland & Thomas saw frequent leg-waving when spiders were alone in field and in clean boxes; Bonnet saw waving only before ♀♀. |
| Differs from courtship in quiet palps & absence of low stage. At close quarters, chelicerae open, 1st legs spread widely, often touch opponent's; no injuries. Displays freely to mirror. | 1st legs elongated, darkened. Clypeus & palps with buffy yellow bands against black. | Basically a runner although jumps readily over gaps; 1st legs little used in walking, habitually waved during pauses; true also of ♀♀ & young. ♀ raises 1st legs & vibrates palps during display. |

TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Name | Display References | Courtship Posture (Stage I) |
|---|---|---|
| | PLEXIPPINAE | |
| *Plexippus paykullii* Aud. | Crane (unpublished obs.); Pl. I, fig. 1, this paper. (Venezuela) | Carapace very high.<br>1st legs stretched forward, up & out at varying wide ∠s, higher with excitement; no waving.<br>Palps quiet.<br>Abdomen pendent.<br>Prolonged posing in display position. |
| *Eustiromastix* sp. | Crane (unpublished obs.). (Venezuela) | Carapace high.<br>1st legs raised antero-laterally @ ∠ of 45° to ground; sometimes jerked, & raised higher.<br>Palps vibrate.<br>Abdomen horizontal.<br>Some posing in display position. |
| *Saitis barbipes* Sim. | Berland, '23, p. 206.<br>Berland, '27, p. 15; fig.<br>(France) | 3rd legs wave. |
| *Corythalia xanthopa* Crane | Crane, '48.1, p. 35; figs. (also, see footnote, this paper, p. 183).<br>(Venezuela) | Carapace moderately high.<br>Palps hanging, motionless.<br>Abdomen slightly below horizontal.<br>Stage Ia: Side-to-side rocking, all feet on ground.<br>Stage Ib: 1st legs stretched forward, straight, parallel @ ∠ of 45° to ground.<br>No posing in display position. |
| *Corythalia chalcea* Crane | Crane, '48.1, p. 21; figs.<br>(Venezuela) | Carapace moderately high.<br>Palps hanging, motionless.<br>Abdomen about horizontal.<br>3rd legs stretched out, waved up & down in unison above the horizontal.<br>No posing in display position. |
| *Corythalia fulgipedia* Crane | Crane, '48.1, p. 28; figs.<br>(Venezuela) | Carapace progressively lowered.<br>Palps jerked in unison.<br>Abdomen about horizontal.<br>1st, 2nd, & 3rd legs stretched far out to sides, the 3rd legs being slightly intermittently raised & vibrated up & down in unison with body.<br>No posing in display position. |

TABLE II (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Threat Posture & Fighting | Principal Apparent Morphological Adaptations to Display | Locomotion & Remarks |
|---|---|---|
| | PLEXIPPINAE (cont.) | |
| No inter-male displays seen.<br>Mirror response not tested. | 1st legs elongated, enlarged, darkened.<br>White clypeus band against black. | Hops often even during ordinary progress.<br>♀ completely passive. |
| Scarcely developed; rarely, brief threat similar to early courtship but abdomen lowered & palps quiet.<br>Occasional brief mirror display, sometimes ending in attack. | 1st legs slightly longer, thicker, blacker than others. | Hops often even during ordinary progress.<br>1st legs take active part in walking.<br>Palps quiet.<br>♀ extremely savage both before & after mating; often kills ♂. |
| Same as courtship. | 3rd legs elongated, compressed, fringed. | Performs display motions even when alone in clean boxes. |
| Completely distinct from courtship.<br>Carapace very high.<br>Palps motionless, flexed, their yellow scales continuing band of clypeus.<br>Abdomen pendent.<br>2nd, 3rd & 4th legs off ground, raised successively higher.<br>Prolonged posing. No fighting.<br>Displays freely to mirror. | Palps & clypeus with yellow bands.<br>2nd, 3rd & 4th legs fringed, compressed, with iridescent patches; 3rd & 4th legs elongated. | Ordinary progress consists largely of hopping.<br>1st legs take active part in walking.<br>Palps quiet.<br>♀ not aggressive; when watching display, sits high with braced legs until receptive, then crouches. |
| Distinct from courtship, although same legs used.<br>Differs in waving 3rd legs *below* horizontal, often in an arch; prolonged posing.<br>Palps flexed & stiff.<br>No fighting.<br>Displays freely to mirror. | 1st, 2nd & 3rd legs fringed, compressed, with iridescent patches; 3rd legs elongated. | Locomotion as in *xanthopa*.<br>♀ sometimes aggressive, may do some form of reciprocal display. |
| Distinct from courtship, although similar in very first phase, & same legs used throughout. Whereas in courtship carapace sinks lower, in threat it rises higher. At peak, all legs are drawn close in & stretch up, 2nd tarsi leave ground & 3rd legs are raised slightly; body rocks from side to side; posing with 3rd legs arched frequent.<br>Palps jerked at beginning, later flexed & stiff.<br>No fighting.<br>Displays freely to mirror. | 1st, 2nd & 3rd legs fringed, compressed, with iridescent patches strongly developed; 3rd legs elongated.<br>Palps with white patches. | Locomotion as in *xanthopa*.<br>♀ more aggressive than most salticids, although not seen to injure ♂; when stimulated performs rough, reciprocal display. |

TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Name | Display References | Courtship Posture (Stage I) |
|---|---|---|
| | MAGONINAE | |
| *Maevia vittata* (Hentz) | Peckham, '89, p. 54; fig. (*"Astia vittata"*) (Wisconsin, U.S.A.) Painter, '13, p. 625. (Connecticut, U.S.A.) | Displays of the 2 forms differ. *Gray form*: Carapace high; 1st legs raised, waved, palps stretched sideways; abdomen down; later, whole body low, 1st & 2nd legs forward, tips touching; palps forward. (Peckham, Wisc.). Low stage precedes high stage. (Painter, Conn.). *Black, tufted form*: Carapace very high; 1st legs raised & waved, or held high in pose. (Peckham & Painter). |
| *Mago dentichelis* Crane | Crane, '49, p. 48; fig. (Venezuela) | Carapace slightly raised. 1st legs stretched sideways & slightly forward; waved alternately up and down or held in pose. 2nd tarsi touch ground, far out & slightly forward. Abdomen sometimes vibrated. |
| *Ballus depressus* Walk. | Bristowe, '31, p. 1409; fig. Bristowe, '41, p. 484; fig. (England) | All legs on ground, drawn in, sways body from side to side. |

under consideration in this paper. Text-fig. 1 and Table III will give some idea of the variety of display motions throughout the family. All displays unite at least several of the listed movements, and many involve all of the major headings except that of retinal motion, which so far appears to operate as part of the signal mechanism only in *Lyssomanes*.

No less varied are the forms of "ornamentation" in the family; these occur too often on displayed appendages to be explained only by chance mutations, metabolic processes, other behavior patterns, etc. They include many specializations of size, shape, hair concentration, scalation and pigmentation, several forms usually occurring in a single spider. For example, the first legs, which always enter at least into Stage II courtships, are often elongated, thickened and much darker than the others; in addition, the palps, which frequently vibrate during display, in many species show patches of shiny white scales. Again, in *Corythalia xanthopa*, the fourth legs, elevated only in threat display, are prominantly fringed; in the related *C. chalcea*, in which they never leave the ground, fringes are absent. Many other examples occur in the literature, of which the Peckham's original series are among the best (1889, 1890). The striking point is that any appendage specially exhibited in epigamic display usually shows some differentiation which is to human eyes conspicuous.

However, two other obvious points must be kept in mind. First, not all parts active in display are so ornamented; an example is the brown abdomen of *Semorina*, relieved only with small, pale inconstant spots. Second, not all parts conspicuously ornamented (again, to human eyes) play any demonstrable part whatsoever in display. Examples are the bright scarlet abdomen of *Phiale flammea* and the striking carapace bands of various *Phiale* and *Corythalia*.

## B. Historical Review.

The history of the study of salticid display reflects the changing ideas of evolutionists. The Peckhams pioneered both in the recording and explanation of epigamic display and of the apparently correlated ornamentation (1889, 1890). According to them, the phenomena were due to direct Darwinian sexual selection; the females, consciously or unconsciously, were affected by the performances, colors and beauty of the males, selecting the most handsome or at least the most striking. Male battles were initiated both for simple possession of a mate and as sham contests for the females' edification. The Peck-

TABLE II. (cont.)

Comparative Display Data in Seven Subfamilies of Salticid Spiders.

| Threat Posture & Fighting | Principal Apparent Morphological Adaptations to Display | Locomotion & Remarks |
|---|---|---|
| | MAGONINAE (cont.) | |
| Wave 1st legs at each other but "quarrels . . . harmless" (Peckham). Displays to mirror. | Tufted form is black anteriorly, has cephalic tufts. | Peckham & Painter disagree on selection value of dimorphism. ♀♀ irritable; fight each other. |
| Stage I: Similar to courtship. Stage II: 1st legs waved higher, almost meet overhead; when lowered, 1st & 2nd tarsi rub together. Rarely, chelicerae opened and knocked repeatedly against opponent's; no injuries. Displays to mirror. | 1st & 2nd legs enlarged, blackened. | 5 other Venezuelan magoninids use all legs actively in walking, hop freely during ordinary locomotion. All include rubbing of 1st & 2nd tarsi in display. ♀ usually extends 1st legs during courtship. |
| | 1st legs enlarged, partly blackened. | ♀ vibrates light palps. |

hams disagreed strongly with Wallace (1878, 1889), who attributed both performance and ornamentation to the greater vigor of the male, especially during the breeding season. Montgomery (1910) in general held Wallace's views; furthermore, he thought the displays originated in self-defense movements, which were combined with external evidence of physiological excitement. Berland (1923, 1927) attributed the behavior altogether to the exceptional physiological activity of the breeding season and its correlated excitement.

Bristowe (1941 *et ante*) has held the view that courtship in spiders in general has two fairly distinct functions, namely recognition and stimulation. Recognition he holds to be particularly important, since in spiders the female is not only carnivorous but often much larger than the male. Inter-male display and fighting he attributes essentially to mistaken identity: "It, would appear from what has been said above that the battles, which are preceded by normal courtship reactions, are the outcome of frustrated instinct, and are modifications of courting procedure brought about as a result of the different reception experienced at the hands of another male to that of a female." (1929, p. 352). He believes that display arose from the groping and chemotaxing motions of primitive spiders, which have been modified by signs of sexual excitement, such as twitching of the abdomen. He points out that a male which produces a striking pigment spot easily visible to the female during his approach has a better chance to survive than has an individual less easily identified.

Savory agrees with Bristowe, except that he considers the division between "recognition"—for which he prefers the term "realization"—and stimulation invalid. He gives the following summary of his views on spider courtship: "If we may venture to summarize in a few words the results of so complex an activity as courtship, we may say that courtship is a chain of related instinctive actions, in which the reproductive urge suppresses the normal habits of self-protection and self-nourishment, and is accompanied internally by the physiological changes necessary to make the subsequent union possible." (1928, p. 221).

Gerhardt, who has recorded numerous spider pairings, has been most interested in copulation methods, showing that the various positions assumed by the male shed light on phylogeny. In salticids the copulation position is invariably dorsal and similar throughout the family. He has made few observations on the courtship phases of reproduction.

There has been as great discrepancy in

views regarding the senses involved in salticid display, as in those concerning its origin and functions. The Peckhams (1894) concluded that sight was essential, both for recognition and as stimulus for display; Petrunkevitch (1910) agreed. Montgomery (1910) apparently saw a salticid court after merely touching a female. Berland (1914, 1923, 1927) thought smell must be involved in locating the female though sight was needed to stimulate courtship. Bristowe and Locket (1926) and Bristowe (1929, 1941) thought that both sight and chemotaxis (referred to as "smell" in the earlier papers) were involved. Savory (1928, p. 215), after speaking of inter-male courtships, of the courting of immature individuals and those of other species, sometimes through glass, says in regard to spider courtship in general: "It is clear, therefore, that the stimulus which initiates the male's performance is vague, rather than definite and specific. It may act upon the sense of sight, of smell, or of touch, but the appearance or the scent of the female does not seem to be readily distinguishable from that of the male."

The most recent group of observers have concluded, along with the Peckhams and Petrunkevitch, that sight alone among salticids is the only adequate and necessary stimulus for salticid display; these workers include Homann (1928), Bonnet (1933), Heil (1936) and Kaston (1936). The latter gives a detailed review of previous work, followed by a report and discussion of observations and experiments of his own; these were conducted on thomisids, pisaurids, lycosids and salticids. His salticid examples are distributed among four Connecticut species of the genus *Phidippus* (Dendryphantinæ). His conclusions, which include his results with that genus, are as follows (p. 152): "On the basis of a large number of observations and experiments with the males of 19 species from 4 families of vagabond spiders, it is pointed out that the senses involved in courtship may vary with the species. There is no evidence that a sense of smell is used in sex recognition by any spiders. At least this sense plays no part in initiating courtship activity in the male. There is no evidence that Attid males can 'recognize' the females by any sense other than sight. At any rate, it appears that the visual stimulus is the only one that suffices to incite courship in this family."

### C. Bases for Disagreements.

The disagreements and uncertainties among previous investigators appear to have been due principally to the following causes:

1. Although all observers have realized that display stimuli *among* the various families differed, and were roughly dependent on the development of vision, yet it does not seem to have been clear that there are large differences *within* the family, at least in salticids, in the relative importance of the senses. On these sensory differences depend many differences in behavior.

2. Systematic attention does not seem to have been paid to the fluctuating physiological states of individual spiders.

3. The early experiments, as usual throughout the history of biological science, were not properly organized to ensure the testing of only one stimulus or characteristic at a time.

4. In later work, the compound natures of such concepts as "visual stimuli" do not seem to have been taken fully into account.

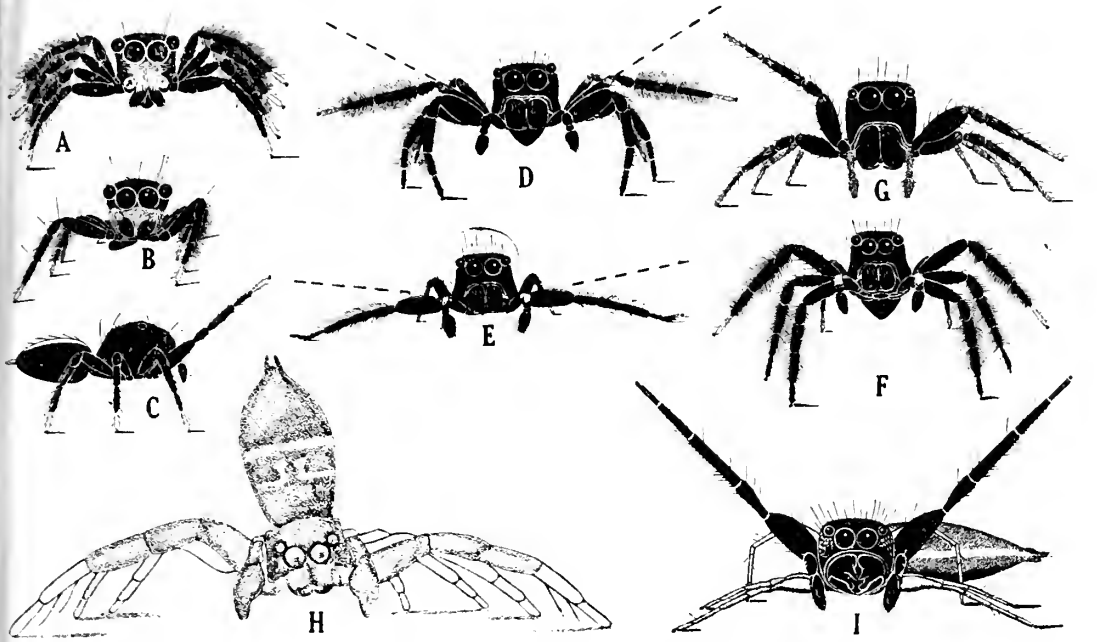
5. The recent concepts of innate releasing and directive mechanisms, as developed by Lorenz, Tinbergen, and their co-workers, do not appear to have been applied to spiders.

6. Certain motions involving sensory perception, such as waving of the first legs, have perhaps occasionally been mistaken for epigamic display.

TABLE III.

Principal Motions Reported in Salticid Display Literature.

1. General manoeuvers, involving spider as a whole.
   a. Tacking.
   b. Direct approach.
   c. Leaping.
   d. Sidling.
   e. Semi-circling and circling.
   f. Posing.
   g. Crawling.
   h. Elevation of carapace.
   i. Rocking motions.
   j. Bouncing motions.
2. Retinal motions within antero-median eyes.
3. Palp motions.
   a. Vibrations, jerks, rotations; synchronized or alternate.
   b. Flexion or extension in special attitudes.
   c. Palpation of female or opponent.
4. Chelicerae motions.
   a. Lateral extension of basal segment.
   b. Extension of distal segment.
   c. Clinching.
   d. Biting.
5. First leg motions.
   a. Elevation and extension forward, up or out, and to any intermediate degree.
   b. Vibrations, waves, jerks, rotations; synchronized or alternate.
6. Second leg motions.
   a. Extension forward, to rub second tarsus against first.
   b. Elevation to form portion of fan-type display.
7. Third and fourth leg motions: Elevation and extension to various degrees, sometimes forming part of fan-type display involving all legs.
8. Abdominal motions.
   a. Depression, when carapace is raised.
   b. Twitching or vibration; vertical or horizontal.
   c. Twisting or bending to side.
   d. Elevation.




TEXT-FIG. 1. Examples of display motions in salticid spiders. A-F, Subfamily Plexippinae; G, Magoninae; H, Synagelinae; I, Dendryphantinae. **A**, *Corythalia xanthopa*, threat; **B**, **C**, same, courtship; **D**, *C. chalcea*, threat (dotted lines indicate peak position of legs during courtship); **E**, *C. fulgipedia*, threat; **F**, same, courtship; **G**, *Mago dentichelis*, courtship; **H**. *Gertschia noxiosa*, courtship (from Connecticut, U. S. A.; similar to that of the Venezuelan genus *Semorina*); **I**, *Ashtabula furcillata*, courtship. **H**, after Kaston, 1948; others reprinted from Parts I and III.

7. The great range of development of threat display within this single family does not appear to have been recognized, since the days of the Peckhams' scattered remarks on the subject.

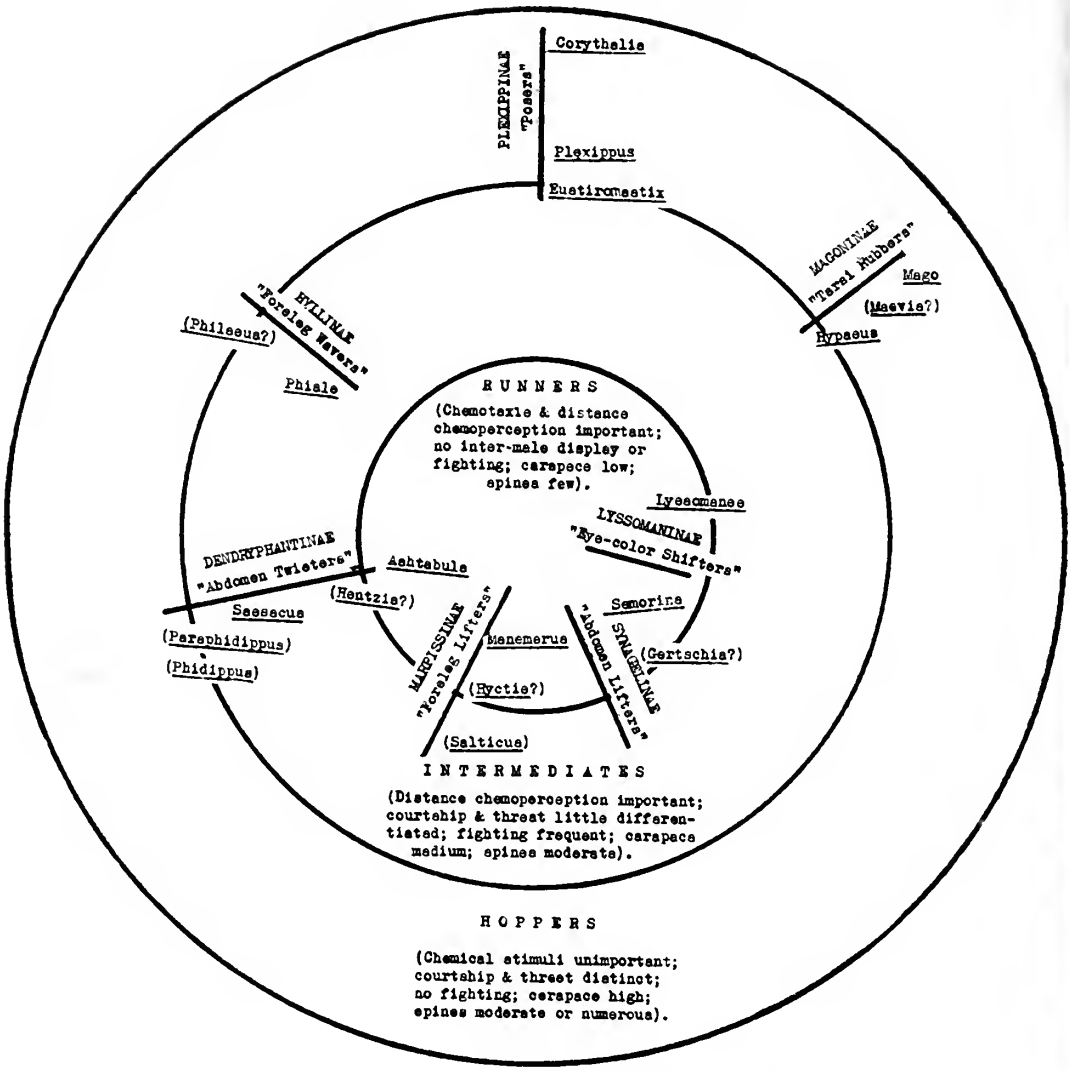
D. PROGNOSIS OF EVOLUTIONARY PATTERN.

In order to bring into perspective the material in the following pages, it is necessary to anticipate some of the conclusions reached not only in this paper but in future sections of the series on post-embryology and general evolutionary trends.

1. *Correlation of Jumping with Sensory Development.* The genera studied at Rancho Grande showed great variety in the frequency of jumping in the course of normal, unexcited progress. Taking into consideration their behavior in other fields, notably display, it seems certain that this variety is based on differences in the dependence on various senses. In some forms more dependence is placed on chemical senses and less on vision. Evidence is presented later showing that these chemical senses include both chemotaxis and a distance chemoperception appearing very similar in its operation to the vertebrate sense of smell. In other forms, vision seems both more acute and more farsighted, while the chemical senses are relegated to relative unimportance. Experiments have not yet been performed at Rancho Grande on variations in visual acuity, although several experimenters, notably Homann (1928) and Heil (1936), present modern data on visual perceptions in species of the subfamilies Marpissinæ and Hyllinæ.

A few minutes' observation of unconfined salticids of selected genera will, I think, give convincing empiric support of the hypothesis. For example, in *Ashtabula* the progress is "a scurrying run, the first legs held flat and low, straight in front of the body; both they and the palps palpate the surface almost constantly during progress. During pauses the first legs are usully elevated, and they and the palps jerked rapidly up and down." (Part III, 1949, p. 41). These "runners," as salticids of similar habits will be called, never resort to hopping or jumping except in crossing gaps in the surface and in the final stages of prey capture. In contrast to other kinds, they are more easily observed in glass-covered dishes than when permitted to run freely on a table (cf. Part II, p. 143). Their comparatively poor vision and their dependence on chemotaxis, or near-chemotaxis, make their exploration of a new environment a highly "restless" and "nervous"-appearing proceeding, as they race to and fro.

In strong contrast is the behavior of an almost completely vision-dependent salticid, such as a *Corythalia*. When allowed to drop on an unfamiliar surface, he tends to pivot almost where he is placed while he looks all around; finally he moves off, without haste or




TEXT-FIG. 2. Tentative basis for a hypothetical phylogeny in salticids. See text (pp. 205 and 175) for explanation; cf. Table II. Non-Venezuelan genera are enclosed in parentheses; those not observed alive by the author are followed by a question mark. The characteristics ("foreleg lifters" etc.) under each subfamily indicate the most generally present display distinction; it usually is not found in every genus, and occurs sporadically in other subfamilies as well; cf. Lorenz (1941) on the phylogeny of display in ducks.

visible agitation, in a series of short runs and hops, interspersed with pauses for further observation. His palps, usually motionless, are held quite clear of the ground; his first legs are used as much in walking as all the others. To the human observer, in an anthropomorphic moment, the contrast in "poise" between a chemotaxis-dependent and a strongly vision-dependent salticid is ludicrous. When startled or pursued he hops almost altogether. In the future, salticids progressing in the *Corythalia* fashion will be called "hoppers."

*Phiale* is a good example of an intermediate stage, in which hopping is moderate and eyesight obviously keen. Considerable dependence appears to be placed on distance chemoperception, however, although not on chemotaxis. The specially sensitive first legs and palps are often carried up, in normal progress, and during the pauses they are waved up and down, without touching the ground; it seems certain that they are receiving sense impressions which, by definition, are not chemotactic.

Characteristics of locomotion, where known, are included in Table II.

2. *Preliminary View of Evolutionary Pattern.* It is generally agreed that the salticids are more specialized than the lycosids, particularly in regard to the development of vision. In this characteristic, indeed, they lead all other families. It seems likely, therefore, that the salticids in which vision is

best developed are those farthest from the primitive stock. This hypothesis is supported by evidence from a number of other fields, although the pattern of specialization, as shown even in these few present-day genera, is far from a simple "family tree." As in all other groups, salticids having many primitive characteristics may be extremely specialized in a few directions.

Briefly summarized, the hypothetical pattern may be stated as follows:

The evidence in regard to salticid evolution—based on post-embryology, external morphology, ornamentation, locomotion, general habits and epigamic display—all points to a radiative type of development. Many forms with primitive characteristics still survive. Each subfamily so far studied in any detail includes genera ranging through at least two stages (Text-fig. 2).

The first, most primitive stage includes species with low carapaces (Text-fig. 3), low visual acuity, high dependence on chemotactic stimuli, locomotion of the running type, courtship simple and threat display absent.

The second stage is characterized by intermediate carapaces, visual acuity, hopping proficiency and courtship development; by depending on distance chemoperception rather than on chemotaxis; and, especially, by the presence of threat display which is based on the mistaking of males for females, and is undifferentiated from courtship except that it often ends in true fighting.

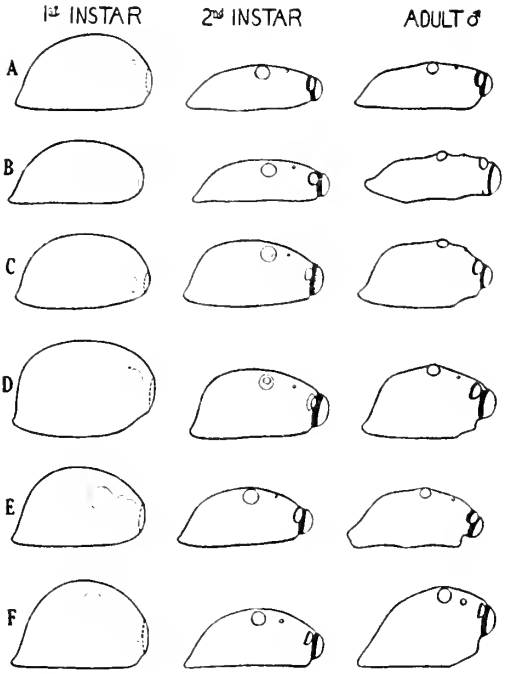
The third and most specialized stage is represented by species with high carapaces, extreme visual acuity, chemical perceptions of minimized importance, locomotion consisting principally of hops, courtship often complex but sometimes secondarily simplified, and threat display separate from courtship and altogether ritualistic.

I realize keenly the extremely small number of forms investigated at Rancho Grande in relation to the large size of the family. However, published records, in so far as they can be analyzed from modern points-of-view, and my own sporadic observations in other localities, appear to lend support to the hypothesis. It seems that the basic framework will prove to have validty.

## V. FACTORS IN DISPLAY.

The releasing and directive mechanisms of salticid display have proved much more varied and their interrelationships more complex than was expected. Although all epigamic display is fundamentally visual in this family, chemoperception is important in certain phases; simple adulthood is not the only physiological essential for performing or responding to display; vision itself must be divided into perceptions of motion, distance, size, form, intensity, pattern and color for an approach to understanding display stimuli.

In the following pages an attempt is made to isolate and evalute these factors, giving




TEXT-FIG. 3. Change of carapace proportions with growth in representative genera of salticids. Left column, 1st instar; center column, 2nd instar; right column, adult male. **A**, *Menemerus bivittatus;* **B**, *Semorino megachelyne;* **C**, *Sassacus flavicinctus;* **D**, *Mago dentichelis;* **E**, *Phiale flammea;* **F**, *Corythalia chalcea.*

in each case a summary of the observations and experimental results upon which the conclusions are based. Because of space limitations, it is impossible to publish full details of field and laboratory data; however, descriptions of especially illustrative observations and experiments are quoted now and then directly from the original notes. Laboratory procedures have already been described (Part II, 1948.2). Reference to Text-fig. 6 will help clarify the relationships of display elements during the course of this analysis; in the subsequent section on innate releasing mechanisms, beginning on p. 199, these factors are viewed as closely integrated, mutually dependent series of stimuli activating, controlling and directing both courtship and threat.

### A. FACTORS OF THE INTERNAL RELEASING MECHANISM.

1. *Age.* In general, no sexual interest appears between the sexes until both are adult. Exceptions occur when a mature male in a particularly responsive state briefly courts a pre-adult female of similar appearance to the adult; such displays never pass beyond Stage I. A number of workers have reported behavior of this kind and I have seen it in various genera, always of the hopper type, especially in *Corythalia.* Very rarely juvenile individuals perform abortive displays; examples will be given below.

The Peckhams (1889, p. 50) recorded the interesting case of *Philaeus militaris* (= *Paraphidippus marginatus*) in which the adult males actually kept guard over individual preadult females until they molted. The nearest approach to this seen at Rancho Grande was the behavior of a single male *C. fulgipedia*. He was captured clinging to the outside of a cocoon, within which a female was molting to the adult instar. He did not even wait for her to dry and harden, but raced through the briefest display as she emerged, and mated. She was still soft and weak, and gave no resistance or apparent response at all. The eggs appeared on schedule, some two months later, and were fertile. This was an exception to the general behavior pattern of the genus.

Similarly, mature males rarely display to juvenile males except in reinforced experimental situations.

During experiments on display sign stimuli with *C. xanthopa* and *C. chalcea*, several cases of display behavior were noted in immature individuals of both sexes. They were exceptions, however, to the rule. Once a preadult (6th instar) male *chalcea* leapt repeatedly on a dead, mounted adult male, when the latter was appropriately moved. He then gave a medium complete threat display, through the fan stage with stiffened palps, following this with a Stage I courtship, and ending with a clumsy attempt to mate, approaching atypically from the rear. When a normal adult male was presented to him, without a rest period, the young one at once gave a complete threat display; when the adult responded in kind, the other retreated. When a preadult female was presented to the young one, she attacked him, whereupon he retreated, turned and courted briefly, Stage I. This sequence with the female happened four times, she charging him each time.

A single case of display in a 5th (pre-preadult) instar *chalcea* was recorded. This individual did a moderately complete threat display (through the arch phase) to two different adult males, punctuating them with retreats. One of the adults responded with threat. There was no courting or other reaction to females.

Preadult females of both *xanthopa* and *chalcea* gave incipient threat displays on a number of occasions, to adult displaying males, alternating the rudimentary fan-pose with the usual abortive attacks and retreats. In each case, it was clearly rudimentary threat, not courtship. These motions were never made in the presence of potential prey or predators, even of similar size.

Display is usually delayed, however, even after the final molt has taken place. *Corythalia* males normally do not display to each other or to a female until at least two days thereafter. One exceptional *xanthopa* did his first threat displays on the third and sixth days, but did not court at all until the seventh and then only a rudimentary Stage I; full threat and courtship were not attained until the tenth day. Although freshly molted females are both attractive and receptive, they normally do not emerge from their cocoons for two or three days. Judging by the responses of males, female *xanthopa* do not attain their maximum attractiveness until about the fifth day.

The age at which males and females lose interest in display varies with the species. After two months in the adult stage, unmated *C. fulgipedia* males usually cease to initiate display in threat or courtship, and do not respond to threats of other males. However, one example, reared from the egg, three months after the final molt briefly courted an aged female who had completed molting more than six months before. Unmated males of *C. xanthopa* are in their adult prime less than a month; for several weeks thereafter they may respond to stimulus situations which are both complete and reinforced, but never to the extent of carrying a courtship beyond Stage I. An exception was a 32-day-adult male which mated with a 33-day-adult female, after a courtship of 13 minutes; the usual courting period for the species is three to five minutes. Their healthy brood was reared through several instars.

Unmated females of *fulgipedia* remain attractive to males and will accept them at least four months after the final molt, even though they have, at the usual time (about two months after molting), started laying the customary successive clutches of eggs. Females of *xanthopa* start losing both their responsiveness to display and their attractiveness after about three weeks, although the eggs in this species are not laid until about the fortieth day after molting.

No Rancho Grande female, in spite of repeated attempts on a number of well-distributed genera, was ever found to mate more than once, when more than a few hours had intervened; usually, also, she lost most of her attractiveness. However, there are a number of recorded northern observations of repeated salticid matings by both males and females (e.g., Peckham, 1889, p. 38). Rancho Grande males, as in the north, copulated readily at least several times in *Corythalia*, *Phiale* and *Menemerus;* other genera were not investigated, nor were such aspects as the duration of fertility and the effect of copulation on subsequent display initiation and duration.

2. *Fluctuating Epigamic Rhythm.* Not only is the period of display and acceptance at Rancho Grande limited to moderately young adults of both sexes and to unmated females, but there is also a definite fluctuation in both sexes from day to day in sexual aggressiveness and receptivity. Such fluctuations are of course well known, and are in fact the rule in higher vertebrates. Hints of it have also been detected in fiddler crabs (Crane, 1941, p. 153 ff.), but it does not seem to have been much investigated in invertebrates.

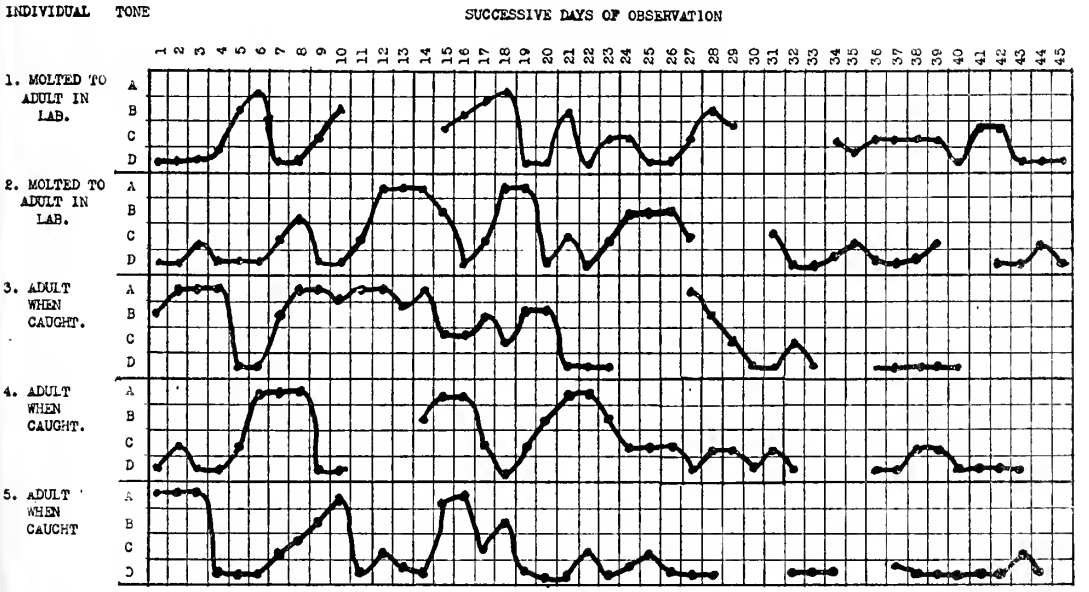
In all salticids under special observation at Rancho Grande, it was noted repeatedly that young, vigorous adults of either sex varied daily in behavior. Those which were particularly lively in display or responsiveness on one day might, on the next, be altogether unresponsive to sexual situations, although their general health and activity seemed unimpaired. These individuals had not been allowed to mate on the preceding day, nor had there been a break in the feeding routine, or noticeable changes in other conditions such as moisture or general weather. A day or more later, they might recover all their previous epigamic energy.

This phenomenon was specially investigated in more than twenty adult *Corythalia xanthopa* males of varying ages. About half of them passed the final molt in the laboratory, so that their exact length of adulthood was known. None of this group was allowed to mate. All were kept under conditions as similar as possible, although all twenty were not observed simultaneously, but in small, overlapping groups. All were tested for various periods up to 43 days with stimuli of such proven efficacy that they came to be termed "standard stimuli" for the species. They consisted of a particular, normal male, dried and mounted in semi-threat stance (see p. 169), a mirror image, young and older adult females, and live normal males.

In the case of low-threshold males, various unnatural or incomplete stimuli were also presented. The mounted specimens and mirror were each presented in a series of up to a dozen successive jerking approaches to the tested male, after his attention had been caught by the stimulus. The quickness of response (if any) was taken into account when determining his sexual tone, because, obviously, a stimulus which drew a response only on repetition was reinforced by summation. Again, the "startle" element of repeated presentations of the same stimulus in quick succession, rather than continuously, was important in drawing responses from low-tone individuals; hence all hand-controlled stimuli, for the sake of uniformity, were presented in this fashion: the mount or mirror was lifted high in the air for an instant after each approach to the spider. The working of the law of heterogeneous summation (Tinbergen, 1948, p. 35) was minimized by always working with a group in every test period; each individual could thus be tested with one stimulus followed by a rest, yet with a minimum wastage of experimental time. The same general rules were followed in all salticid testing (see also, Part II, p. 143).

In the course of the work, the fluctuating internal drive appeared divisible into four major degrees of sexual tone, with the following characteristics:

A-Tone. Internal drive strong, that is, male with low epigamic threshold. Only minimal stimulus needed for maximal response, which follows promptly and appropriately to all normal stimuli and to many deficient stimulus situations as well. Display follows through swiftly into Stage II in courting receptive young females; old females courted with considerable persistence. Responses continued during a prolonged test-period. No "vacuum responses," however, have ever




TEXT-FIG. 4. Daily fluctuation of epigamic threshold in five male *Corythalia xanthopa*. Spiders of A tone are most responsive to epigamic stimuli, those of D tone unresponsive. The tone was determined by the individual's response to three standard stimuli: his own mirror image, a particular dead male mounted in a semi-threat position, and a young, living female. See p. 177. Blanks in the graphs indicate days when observations were not made.

been observed, in this or any other salticid; that is, no display is performed without some external stimulation.

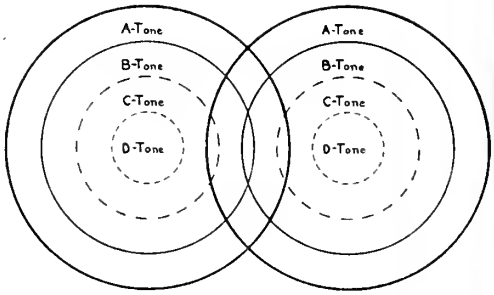
B-Tone. Internal drive moderate, the epigamic threshold being moderately low. Maximal stimulus needed for normal response; either threat or courtship or both may be elicited, but only through summation, though display is eventually complete. Courtship of a young female may be energetically performed throughout its entire course, but older females attract little or no attention. All courtships are likely to die out in the middle, when the male, instead of following up the female during her normal, periodic retreats, simply circles around her previous resting place, palpating the ground in the manner of less specialized, runner-type salticids. Again, the male sometimes gives atypical responses, leaping briefly at the threat stimulus before performing threat display, or even courting it; equally briefly and rarely, he may threaten a female. He may or may not respond to one or two slightly incomplete stimulus situations. Invariably ceases to respond in a test period after relatively few stimuli have been presented.

C-Tone. Internal drive weak, the epigamic threshold being moderately high. Maximal stimulus needed for minimal response. Male responds either to normal threat or normal courtship stimuli, but not both; summative threat stimuli more often draw a response even than young females. No courtship is ever followed through to completion, and the palpating of the female's resting place is pronounced, the male spending much of his attention on one of her former positions, even though she is at the moment sitting in full view, and facing him, only an inch away. Leaping at threat stimuli is frequent and, unlike the case in B-tone spiders, is rarely followed by the normal response. Incomplete stimulus situations attract no attention, except, sometimes, brief notice followed by escape behavior. The attention of C-tone spiders is difficult to attract and hold. they often move about in "restless" fashion, and always stop responding quickly, often after only one or two stimuli have been presented.

D-Tone. Internal drive imperceptible, the the epigamic threshold being very high. Male does not respond with display to stimuli of any kind, although other daily activities, such as feeding and moving about, are unimpaired.

The above four states naturally merge into one another, and in recording the daily changes of tone, it was found convenient to recognize plus and minus degrees. For example, a spider which did not display, but nevertheless showed enough interest to follow a jerked mount or a young female with with his eyes (through the twisting of his carapace), was counted D-plus.

Typical examples of daily fluctuations are shown in Text-fig. 4. Text-fig. 5 diagrams the degree of influence on each other of spiders of various tones.




TEXT-FIG. 5. Diagram showing mutual influence of salticids of various epigamic tones. For example, even an A-tone spider never draws a display response from one of D tone, although he himself displays readily toward individuals of any tone and either sex; B- or C-tone spiders may respond to the displays of an individual of higher tone, but rarely initiate it themselves. The boundaries between tones should not be regarded as hard and fast lines. See pp. 176-179. In salticids, courtships are rarely completed in the field, or threat displays energetically prosecuted, except by spiders of A tone, that is, of the lowest epigamic threshold. This is in contrast to the condition in some vertebrates, where the behavior of a correspondingly low-threshold individual is not regarded as typical (cf. Part II, 1948.2, p. 143, and Tinbergen, 1948, p. 39).

The one result that emerged clearly from the records was the complete lack of a definite rhythm in *xanthopa*. In general, however, individuals in their prime remained from one to four days in A-tone, then dropped within 24 hours to C or D; they remained at these high-threshold levels from one to three days, and then climbed back to B-plus or A in about 48 hours. Some spiders attained A-tone only once in the course of their four weeks of prime, the rest of their top display levels being B's, with prolonged C and D stretches between. A rarely active male, caught adult, had three A-periods of three, four and one day each, during a period of two weeks, with only one day of D intervening; the subsequent portion of his active display prime tapered off in irregularly alternating B's and C's of one to three days each.

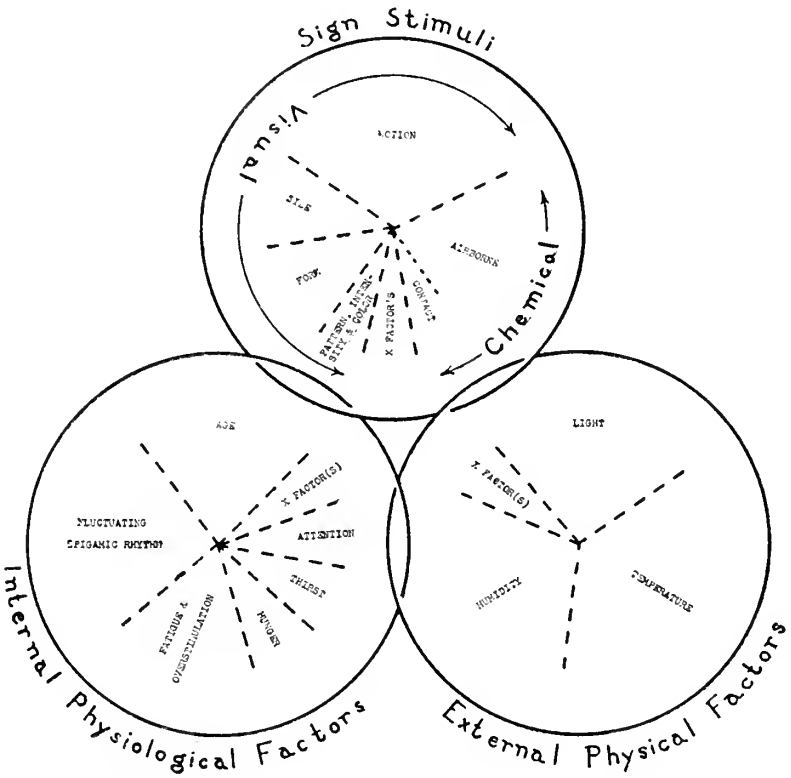
Just-molted males start at D, paying no attention whatever to epigamic stimuli during at least the first two days; they then climb, gradually or abruptly, to their first B or A period, which may come at any time from the third day to the tenth. After about the 28th day, display responses taper off, fluctuating gently between C's and D's. Often they flow along for four or five days on about a C-minus level, responding, for example, one day to a single, summative threat stimulus situation, and the next with a series of leaps only to the same stimulus, but with the addition of a few abortive rocks to a young female.

That the above phenomena are not the results of laboratory conditions is proved by the fact that a number of males were tested

in the field, before capture, and their behavior was found to correspond to that immediately afterwards in the laboratory; also, these and other males were taken, as adults, in all four phases, some young, judging by their future plotted curves, some old. Their behavior curves differed in no wise from those of males reared through at least one molt in the laboratory, except that in general the wild-caught adults tended to hit and hold A-tone oftener and longer.

Although males of other genera and species were not tested systematically, there is no doubt but that they do have periods similar to those of *xanthopa*. Females, too, show noticeable behavior fluctuations, both in general aggressiveness and in reciprocal display, although their periods were not studied. One *C. chalcea*, for example, was especially prone during several days to do a particular type of jiggling in mutual display; I never saw it in another of her species, and it soon dropped from her usual behavior, reappearing only sporadically. Although she was exposed to the display of a number of males during and after this time, she was not allowed to mate for another two weeks, when the process went off perfectly normally.

3. *Hunger and Thirst.* Hunger, as might be expected, was an important factor in the behavior of females, since a hungry female was usually far more aggressive and needed far longer courting than one which was well-fed. However, in no genus except *Eustiromastix* have I ever seen a female try seriously to kill a male, although occasionally she will leap at him. Moderate hunger in males lowers their epigamic tone only




TEXT-FIG. 6. Factors of the innate releasing mechanism in salticid display. The circles are represented as loosely interlocking to indicate the interdependence of the three groups of factors. Similarly, the spokes are not continued to the circumference in order to show the mutual influence of the sections. Finally, the spokes are represented as broken lines, to emphasize the variability and instability of their relative importance; this varies not only throughout the family, but even in the same spider under different conditions. For example, among the Synagelinae, the chemical factors are more important than among the Plexippinae, while the same sections are of still different relative value in the end-forms of the Dendryphantinae. The sizes of the sections, therefore, are merely a guide to their average apparent importance within the family. The term "X-factor(s)" is included in each circle to emphasize the incomplete state of our knowledge. "Distance" is omitted from among the sign stimuli since it seems to be more of a compound factor in display than do the others, based largely on apparent size, on chemical stimuli or their absence, and on physiological conditions; perception of distance and depth does exist however (see Homann, 1928; Heil, 1936). Tactile factors are omitted since they do not release display in salticids, although they are important in the final display stages. The sign stimuli circle applies to courtship; for threat display, the chemical factors should be eliminated.

slightly—from B-minus to C-plus, for example. In all the experimental work, no spiders were tested without having been fed at most 48 hours previously.

Thirst cannot of course properly be separated from the external factor of humidity, although spiders do drink water as needed. Salticids that for some days had been kept without special moisture in the laboratory went into silk shelters, if they did not die first, became semi-torpid and did not react to display stimuli; this behavior is doubtless equivalent to aestivation in the field.

4. *Fatigue and Overstimulation.* These two factors have not been properly distinguished. Actual physical fatigue, however, sometimes appeared clearly involved during experiments. Often initially restless individuals, even of hopper-type genera, were tested which raced about the table before settling down to attending to stimuli; they often had even to be pursued to the floor; afterwards, even when otherwise of A- or B-tone, they always reacted to stimuli for a shorter length of time than those which responded without preliminary activity. On the other hand, overstimulation appears to be a better term for the cessation of reaction that takes place in spiders at the peak of their internal drive, when they have had practically no exercise but have been presented with a succession of stimuli. In every individual the moment is reached, as in other animals, when no further response is drawn, no matter what the stimulus. The length of reaction time is highly variable; *C. xanthopa* is, however, as typical as any: A-tone males may be tested for around half an hour with only minimum pauses between stimuli (about three minutes). When a large group is used (the customary experimental procedure) responses may spread over three or four hours. the long rotation period allowing individual rests of 10 to 30 minutes between stimuli presentations. An individual which is tested in the morning to the point of complete non-response is usually again responsive by mid-afternoon; full recovery (regardless, that is, of internal drive changes) is the rule by the next day. Spiders with low internal drive, e.g., of C-tone, have extremely short response periods, usually totaling only five or ten minutes; often there is only a single response, regardless of length of rest between stimuli.

5. *Attention.* This factor is quite distinct from the others, and a *sine quo non* of display. Although spiders with strong drive undeniably are more easy to stimulate with display situations than weak-drive individuals, all vary irrespective of sexual tone in the amount of time needed to attract their attention to a stimulus. Sometimes they are so restless when first put on the table that their only motive appears to be to get somewhere else; some minutes pass before they seem suddenly to "wake up" with an almost literal jerk and "notice" the stimulus, which may have been equally close in front of them many times before. This applies to both threat and courtship stimuli. The same is true of a spider engaged with one display stimulus, or with food, when another and, at the moment stronger, situation is presented.

### B. Factors of the External Releasing and Directive Mechanism.

1. *Physical Environment.* The effect of the physical environment has not been precisely analyzed in regard to exact tolerances and requirements of temperature, humidity, light and altitude. However, the following facts have been determined:

*Corythalia xanthopa* in the Rancho Grande laboratory displayed readily at temperatures between 65° and 80° Fahr., the extremes tested. As has been noted by others, responses were somewhat accelerated at the higher temperatures. The humidity varied from 50 to 95 per cent. The same species displayed at Weston photometer readings as low as 0.8 foot candles; below that there was no response. During regular experimental sessions, reflected daylight from the laboratory table ranged from about 25 to 75 foot candles, Weston; these readings were comparable to those obtained in *xanthopa's* natural habitat during periods of high activity. *Menemerus,* with apparently poorer vision, seemed to need considerably more light, but no accurate measurements were taken.

*Corythalia fulgipedia, C. chalcea, Eustiromastix* and *Phiale flammea,* although captured at 3,500 feet, all displayed at sea level in New York, having been brought there alive in the early instars. They displayed upon reaching maturity regardless of the month, of the highly variable and unnatural extremes of temperature and humidity in which they had been reared, and of the lower altitude.

Displaying individuals of most species could be found at Rancho Grande from February to September, the period of our residences, which includes most of the dry season and half of the wet. However, as in other groups, most species had a clear peak of breeding adults in May, June and July, the early part of the rainy season.

Both in Venezuela and in New York, spiders displayed under extremely unnatural conditions, with no time whatever needed for adjustment, short of their being literally frozen, deeply chloroformed, dried out or far overheated. That is, if the spider were not injured physically beyond recovery, if he remained capable of primary activities—moving freely, catching prey and spinning a shelter—he could and did display when in a period of moderate or strong drive and when properly stimulated. All salticids observed displayed as readily in a glass container or on a table top as in their own forest environment, and in every case the pattern of display behavior in captivity was identical with that recorded in the field. The only exception was that, rarely, captive

*Corythalia* males, in close quarters under hot lights, occasionally injured each other in actual fights; ordinarily, aggressive behavior was confined to highly ritualized threat display.

In the field, salticids invariably disappeared under leaves and therefore presumably did not display, both during every shower beyond a drizzle and during all hours of intense heat, drought or baking sunlight. Display during the night in the laboratory was successfully stimulated in A- or B-tone *Corythalia* and *Phiale* which were forced out of their shelters and provided with adequate light. Hence an innate diurnal rhythm does not appear to exist in these forms.

In brief, the only external physical requirements for display appear to be tolerable conditions of temperature and humidity, along with adequate light (sun, photoflood or mazda). In *Corythalia* at least, this illumination is less than that sufficient for comfortable reading by a human being.

2. *Sensory Elements and Sign Stimuli.* The sign stimuli (or perceptual signs) considered here are those external signals which are involved in releasing or directing epigamic display in salticids. They are unexpectedly complex, especially in courtship, in which they customarily involve compound tactile, chemoperceptual and visual stimuli. Of them all, only two or three combinations of a few visual stimulus-elements can be termed primary releasers, since no salticid displayed at Rancho Grande unless the antero-median eyes were photopically stimulated.

Reference to Table II and Text-fig. 2 will be helpful in maintaining orientation in regard to the various displays and the presumed degree of specialization of species discussed.

a. *Tactile Perceptions.* Although in many web-spinning spiders tactile perceptions are of great importance in courtship, in salticids their role is confined to advanced Stage II, where the stimuli are probably mingled with chemotactic stimuli. They will be discussed together on p. 182.

b. *Chemoperception.* For many years a possible "sense of smell," as earlier observers called it, in spiders has been the subject of extended experiment and considerable controversy. In their studies of courtship in various spiders, modern workers, particularly Kaston (1936) and Bristowe (1941), have drawn necessary and precise distinctions between contact chemoperception and distance chemoperception.

In contact chemoperception, conveniently called chemotaxis, the spider must actually touch the female herself, her silk or exuviae, or at least her trail, in order to receive a sensory chemical impression. This sense, both authors agree, often enters into spider courtship, although it is not always essential for the stimulation of display, and, in their experiments, was not necessary in salticids. The Rancho Grande results were in agreement with these conclusions.

On the other hand, in courtship stimuli involving distance chemoperception, a spider would have to react to volatile, airborne particles given off by a female, her silk or exuviae, or her trail. Such stimuli have not been found by these authors to take any part in stimulating courtship display in any spiders which they have studied, nor do they consider that evidence has yet been brought forward which necessitates the operation of such a sense in spider courtship. Here the Rancho Grande results differ; it seems necessary to postulate the use as a secondary sign stimulus in courtship of a sense analogous to smell.

The two aspects of chemoperception—contact and distance—will now be considered in reference to the Rancho Grande salticids.

i. *Chemotaxis.* In some other groups of spiders, all with vision less well developed than in salticids, chemotaxis is a primary releaser of courtship, with or without sight of the female. In salticids this is certainly not the case. Kaston, reexamining the situation in 1936 (pp. 129-130), concluded that it was not essential in two species of *Phidippus*, and Bristowe (1941 *et ante*) agreed. Similarly, at Rancho Grande, when chemotaxis was positively eliminated from the stimulus situation, in every genus tested A-tone males displayed without chemotaxis. Contrariwise, no individual ever displayed on the stimulus of chemotaxis alone, although excitement over chemotactic stimuli was often shown. The tested forms were the following: *Menemerus, Semorina brachychelyne, Ashtabula, Sassacus* (2 spp.), *Phiale* (2 spp.), *Plexippus* and *Corythalia* (3 spp.).

However, in all of the numerous observations and experiments, variations were very obvious in the minor exercise of chemotaxis. These were present on all levels—generic, specific and individual. When chemotaxis was allowed, the initiation of display in all the runner genera (*Menemerus, Semorina, Ashtabula*) was definitely expedited, although that of the hopper and intermediate forms (e. g., *Corythalia, Phiale*) was apparently not affected in the case of A-tone spiders. However, many individuals in all genera, when of B-tone, initiated display only when chemotaxis was included in the stimulus situation.

Salticids of all conditions, except those of D-tone, and in all genera, but particularly among the runners, often paid great attention to the recent resting places of females, tapping them with palps and forelegs and revolving round and round the area. All B-tone or tiring spiders tended to break off display and palpate at length her just-vacated resting spot even as the aroused female sat and watched only an inch or two away; sometimes, absorbed in these palpations, a male allowed a prospective mate to wander completely out of sight; this reaction was noted

most frequently in the hopper genus *Corythalia.*

In the runners there was more of a tendency to follow a trail, by intermittent palpation of the ground, over which the female had passed. In *Sassacus ocellatus*, *Phiale* and *Corythalia,* there were no tendencies to trail-following chemotaxis at all; once a female had attracted his attention, a male often followed her zigzag or curving retreat by taking the most efficient short-cuts, whether or not display had been initiated.

The latter half of Stage II is so similar and well known throughout the family that it will not be specially treated here. It begins with the male climbing over the female, patting her carapace with palps and first legs, and follows through to the twisting of the abdomen and successive insertion of the palps into the epigynum, usually after some palpation of its surface. Here it will only be pointed out that chemotactic as well as purely tactile perceptions are probably involved.

Chemotactic perceptions are also not necessarily eliminated from the stimuli which continue to lower the female's threshold during the same period. Her final resistance is probably broken down by the stimulating action of the patting motions; however, since her chemotactic receptors appear to be scattered over her entire body, as well as concentrated on the appendages (Kaston, 1936 & ref.), they very likely are stimulated at this time.

Except in the advanced stage noted above, chemotaxis certainly plays no important part in the acceptance of a male by a female. Since she usually retreats a number of times during normal courtship, she infrequently crosses a male's trail during display in the field. It is true that some individual males have a tendency to circle the female completely during display. Also, females of *Phiale* and *Menemerus* have often been seen to palpate a male's recent resting place, while he is still displaying. Nevertheless, on open table tops in more than 20 experimental situations and in uncounted casual observations, involving all the experimental genera, males were accepted without the females once crossing their trail.

I can find no evidence whatever that chemotaxis plays any part in inter-male display; I have never seen a male palpate the surface or show apparent excitement of any kind when placed on the spot recently vacated by another male, even when both have been or are displaying to each other. However, a male *Menemerus,* a typical runner, could be induced to display to his mirror image only by corking him in a clean glass vial and holding the mirror against the glass end. After a few minutes, display sometimes took place in A-tone individuals, each presumably activated by his own strongly reinforced chemical stimuli. This experiment was performed on six different males; the display was indistinguishable from Stage I of courtship and was always of very brief duration.

The occasional males in various genera that enter upon Stage II of threat, when the first legs of each opponent touch, practically always finish the encounter at this point with no damage done to either. The fangs are very rarely unsheathed during these moments. Chemotaxis, or, rather, the absence of the female chemotactic stimulus, may be involved here.

ii. *Distance Chemoperception.* The apparent part played in display by a sense analogous to olfaction will now be discussed. The majority of previous experiments concerned with it have dealt with the reactions of spiders to essential oils, chiefly of an apparently irritating nature. It has been pointed out several times (e.g., Kaston, 1936, p. 146) that sensitivity to these stimuli does not necessarily indicate possession of a true olfactory sense. Such a sense has, however, been proved to occur in a number of terrestrial invertebrates, including moths, beetles and bees. The only aspect directly concerned in the present display study is the part, if any, taken by a sense analogous to odor perception.

If such a sense exists, the necessary affectors do not, of course, necessarily consist of volatile particles; they need only be airborne and, presumably, invisible to human eyes. It is regrettable but natural that we human beings, as visually dominated organisms, should tend to be impressed with and to study chiefly visually or at least aurally dominated displays in animals. Moths and other nocturnal creatures, both vertebrate and invertebrate, may, for all we know, give off in epigamic display regular symphonies of smells in a rhythmic succession. More difficult to imagine, but perhaps easier to check, is the following possibility: Females of certain animals, at the peak of physiological readiness, may actually radiate certain wavelengths invisible to us. These may be either infrared or ultraviolet, using those terms in their broadest sense. An alternative possibility is that these frequencies may be reflected rather than radiated. The emission, of whichever type, would doubtless be under hormonal control, and would have some signal values for males. It would not necessarily of course be perceived visually. In that connection may be mentioned the old, recurrent speculations on possible wave-perceptive functions of insect antennae. The claims of some investigators that blind-folded human beings respond muscularly to red light is another related topic (See Birren, 1938, ref.).

Toward the proof or disproof of the possibility of such emissions, not one jot of experimental proof is offered here. The subject is mentioned only because of its potential connection with salticid display, and in the hope of stimulating investigation. If found valid, it would explain one or more aspects of

animal display which at present are inexplicable. The proving of the perception of special frequencies would solve puzzles in certain fiddler crabs and birds, for example. In each of these cases, males appear instantly to distinguish receptive females of their own kind from non-receptive ones in some fashion which does not appear to depend either on her behavior or on her emission of any recognized sensory signal (see Beebe, 1928, p. 64; Crane, 1941, p. 157; and Armstrong, 1947, p. 340 & ref.).

It is true that the operation of scent has not yet been eliminated under experimental conditions in the above instances. Since the published work on crabs, however, many field examples have been seen where the particularly stimulating female crab was several yards to leeward in a stiff wind; the poor olfactory development in birds is well known. According to Kettlewell (1946), however, moths have not yet been proved ever to approach females with the wind, the contrary evidence of earlier experiments having been due to incomplete observations.

In view of its highly controversial aspect, therefore, this present speculation may be on the order of postulating improbable sunken continents in order to explain an inconvenient distribution of fauna, flora or culture. Nevertheless, it is set down in the hope that adequate instruments will soon be developed capable of testing the possibility. Proofs of the use of supersonic signals by bats (Hartridge, 1945) and the perception of polarization of light by bees (von Frisch, 1949; Thorpe, 1949) are suggestive recent results of research in unusual directions. In our own future researches and experiments we certainly intend to take such possibilities into account.

In regard to salticid spiders, however, it seems that the phenomena described below can be most simply and adequately explained by postulating the action of typical, airborne, volatile, chemical particles acting upon appropriate receptors. They will be so considered in this paper.

The work at Rancho Grande seems to point conclusively to the existence of such a chemical sense. It appears likely that it is merely a further development of chemotaxis, in that the affectors, and perhaps the receptors, are basically similar or identical. This sense plays an important secondary role in courtship.

The evidence for this conclusion is based chiefly on the following observation: Young, living, unmated, adult females at Rancho Grande were in general markedly more successful in drawing courtship display from males than were females in other categories.

Their superior attraction was noted in more than 25 species, in fact, in all material plentiful enough to yield comparative observations; these included all the Rancho Grande forms discussed in this paper. The Peckhams (1894, p. 251) attributed a similar observation to the fact that females about to lay eggs were so heavy that they tended to move about less, and that it was the lack of movement which made them relatively unattractive. In the basic experiments at Rancho Grande, this factor was eliminated by chloroforming the subjects. They were then presented alternately as motionless, or uniformly moving stimuli on L-mounts. Chemotaxis was ruled out as previously described (Part II, pp. 143 and 144). The males were allowed only front views on a plane surface, to avoid the visual variables of large vs. small abdomens, or fresh vs. rubbed patterns. The effects of summation were guarded against, as usual. For experimental purposes, a female was counted as "young" when she had been adult for less than two weeks, "old" when more than four.

The general results, in this and other genera, were as follows: A-tone males, when given a choice, almost always devoted their attention to a young female, although an old or mated individual was usually courted energetically if no other was available. B-tone and C-tone males, as well as all near-senile males, showed no courtship display response at all to any but young females. A-tone males often courted a young female which was chloroformed, placed on a mount and held motionless; males of the same tone rarely took any notice of an old or mated individual similarly presented. Dead, thoroughly dried females of all ages either drew no reaction when motionless, or, when appropriately moved, occasionally drew confused threat display. Finally, although certain paper models of *C. xanthopa* males successfully drew threat display, models of females were never successful.

Special test situations, involving *C. xanthopa*[2] and *Phiale*, gave the following results which are pertinent:

The abdomen of a young adult female *xanthopa* had been painted black for another experiment on the tenth day after her molt. After repeated intermittent chloroforming, she died about five o'clock one afternoon. At that time, when crumpled, motionless and of atypical coloring, she readily drew display from several males. Chemotaxis had, as usual, been eliminated from the test situation. By seven o'clock the next morning, although she was not yet stiff, she had lost attraction for three A-tone males to the extent that, although some attention was paid her when she was jerkily moved, no display whatever was drawn. The normally colored abdomen of a chloroformed female, adult for fourteen days, was then cut off from the cephalothorax

[2] The published description of *C. xanthopa* display (Part I, p. 36) erroneously states that rocking precedes threat as well as courtship; further observation showed that this occurred only in small, closed dishes involving strong reinforcement of chemical stimuli. Normally, rocking does not occur in threat display. See Table II, this paper, for synopsis of threat and courtship distinctions. Also, the threat display figured (l.c., Text-fig. 14 C) represents a moderate phase; in the extreme form the 4th legs are held even higher, well above the carapace, and the second tarsi leave the ground.

and placed on the mount 10 mm. from the dead female. Two males now displayed promptly to the black corpse, following through to attempted mating with it, disregarding completely the normally colored, detached abdomen.

The detached abdomen was then rubbed over a dried, mounted male, which had heretofore always drawn prompt threat display. It drew brief, confused display, with both threat and courting elements, from a male which had threatened it a few moments before, and threatened standard stimuli immediately after (without a rest period). During the test, however, he followed the confused display with a leap at the mount and finished with an abortive attempt to mate.

On another occasion, a male *xanthopa* was threatening a dried male mount. Another freshly detached abdomen of a young female was hidden under a tiny paper tent, 5 mm. to the left of the displaying male which in turn was 50 mm. from the mount. The male stopped threat display, went into a courtship stance and rocked. When the mount was removed, there was no further reaction.

A *xanthopa* male paid no attention to a scrap of black cloth alone on a mount, or to the same cloth with a young female underneath it, with or without motion of the mount. Then a large, dried *Eustiromastix* male was given a yellow clypeal band similar to that of *xanthopa*, and placed on another mount. This stimulus drew prompt threat display when the mount was moved. The piece of cloth was then placed in a heap under the *Eustiromastix*. Threat again followed. However, when the chloroformed female was once more hidden beneath the cloth and the whole placed under the *Eustiromastix*, the test male paid swift attention without display, then vibrated the palps, took a courtship stance, and, finally, after one or two rocks, leapt on top of the *Eustiromastix* and tried to mate with it. This involved such a violent attempt to twist the stiff abdomen that the whole structure toppled over. With a changed sequence of stimuli, the same series was presented to two other males, with similar results, except that the courtship response died out before mating attempts.

Young females of both *Corythalia* and *Phiale*, when painted to resemble males, drew unmixed courtship, not threat, although old painted females drew mixed display (p. 194).

When female epigyna of *Menemerus*, *Phiale* and *Corythalia*, in a total of six individuals, were sealed with paraffin, no diminution in attraction was noted; the attractive substances are probably secreted rather generally by body and appendages; the experiments of Kaston (1936) and others on non-salticids support this idea.

It should be mentioned incidentally that young adult females have a stronger odor to human noses than either males or older females, at least in *Menemerus* and all three species of *Corythalia*. In a series of tests on *Corythalia*, the odor of young females was the only one perceptible to two of five observers; the other three people in every case considered the young female's odor strongest, but indistinguishable in quality from that of males or other females. The latter seemed stronger than the males'. No generic or specific differences were detected, during casual tests with various genera. The terms used in attempts to describe the salticid odors included "spicy," "pungent," and "faintly antiseptic."

Further incidental data, by no means to be regarded as actual evidence for distance chemoperception, include the different methods of using palps and first legs in the various genera (Table II). This seems to be in accord with the various degrees of reliance on contact and distance chemoperception.

The chemoreceptors (including those of chemotaxis and the distance chemoreceptors, whether or not they are distinct), have been shown to be generally distributed on the spider, but concentrated near the tips of the palpi and first legs (Kaston, 1936 and ref.). With this view the Rancho Grande experiments agree. Females without palps or without first legs readily accepted males in *Menemerus* and *Corythalia*. When both palps and first legs were removed, reaction time was slowed in *Menemerus* but not in *Corythalia*. Males similarly handicapped displayed right through to mating attempts. When use of the first legs was the essential part of display, spiders without them would suddenly leap at the female after a prolonged period of attention. This response was specially noted in *Menemerus*. Reaction time was decidedly slowed in handicapped males in initiating courtship, but not in responding to any of the threat stimuli, including the mirror and painted mounts. It was much slower in mutilated runners of the genus *Menemerus* than in the hopper genus *Corythalia*.

In summary, the following conclusions appear valid. At Rancho Grande, distance (airborne) chemoperception is a positive factor in courtship, but not in threat display. A strong, invisible stimulus is given off by young females, serves as a secondary sign stimulus for releasing courtship and is surpassed in importance only by the male's ability to use his antero-median eyes. It appears to have little directive value. When courtship and threat are distinct, the addition of airborne chemical stimuli from a young female to a stimulus configuration tends to change threat to courtship.

b. *Vision.*

i. *Vision as a primary stimulus to display.* Use of the AME (antero-median eyes) by the male is the only single, *sine qua non* of display. The investigators who have experimented with the reactions of blinded male salticids agree that they will not display when the eyes are completely covered, no matter what other stimuli (e.g., contact and airborne chemical stimuli) are present. Apparent excitement caused by other stimuli

has sometimes, however, been observed. The species previously tested are well distributed among a number of subfamilies: *Dendryphantes elegans, Saitis pulex, Phidippus rufus* and *Astia vittata* (Peckham, 1894, p. 248); *Evarcha blancardi* (Homann, 1928, p. 254); *Aelurillus v-insignatus* (Bristowe, 1929, p. 343); *Phidippus clarus, P. audax* (Kaston, 1936, p. 131). Homann confined some of his blinding experiments to the AME, finding that display failed to occur as completely as when spiders were totally blinded.

The present experiments support and extend these previous conclusions. Two males each of *Corythalia xanthopa, C. chalcea* and *Menemerus bivatattus,* all of A-tone, were used. In one of each pair all eyes except the AME were painted, as described in Part II (1948.2, p. 144); in the other, only the AME were covered. After the spiders had apparently recovered from the chloroform (the minimum time allowance was one hour), standard test stimuli (p. 177) were presented on three successive days, unless a positive response was obtained earlier. Regardless of all-negative responses, the paint was then removed and, in tests counted as successful, positive responses obtained to at least one of the standard stimuli within one hour.

In each species, the males with the AME uncovered performed complete display (both threat and courtship, in the case of *Corythalia*) within the allotted period, although their reaction time in general appeared a little slowed. In contrast, those with the AME painted never displayed at all. The latter did, however, show some awareness of moving objects, including females, by shifts in position and slight "following" with the eyes at distances of half an inch or less. This note is typical: "X64 male sat quiet, although he ran and jumped when prodded. Took no notice of X34 female, as she watched him only one-half inch away; although she actually brushed against him several times, even his palps hung quiet. Later he moved off, crossing her trail and very recent resting place without pausing. Finally, when she jumped past him, he did turn toward her; the stimulus, however, could have been a vibration of her jump, rather than either a chemical or visual stimulus. Even in the same vial with her, with all her chemical stimuli reinforced, there was no reaction."

The most interesting result, from the viewpoint of phylogeny, was that *Menemerus,* which appears to depend more on chemotaxis and distance chemoperception and less on vision than *Corythalia,* was decidedly less handicapped by the loss of the AME. He moved around much more actively, and palpated the females' resting places in apparent excitement. No attempt was made by either genus to pursue prey without the use of the AME.

The AME of a single young female *C. xanthopa* were covered. Just before the operation she had allowed a male to reach an advanced Stage II, when the pair was purposely separated. After painting, she refused him and four other actively displaying males which subsequently displayed to her, two or three in succession, on four successive days. One male, on the third day, reached Stage II repeatedly, ". . . but at the least touch, or before, she moved off. Male was very persistent. She did not turn to keep him in view; her palps hung motionless. Since he circled her time after time in displaying, as usual, she crossed his trail frequently during her retreats. She never once assumed the raised-carapace stance so many *xanthopa* females temporarily adopt when attention is gained. He persisted for twenty minutes, then gave up. I cleaned her eyes, introduced the same male within half an hour, and they were mating five minutes later." (Field lab. note.)

No other female blinding experiments were completed through the final stage of obtaining positive mating responses after the AME were uncovered. However, all the indirect evidence—in the observations of others and in my own—points to the usual necessity for the female to see the male before allowing mating to take place.

In summary, use of the AME, and of the AME only, is a prime requisite in salticid courtship.

ii. *Motion.* It seems well established that at least some salticids will not only leap on motionless prey, but will display to a motionless female (e.g., Peckham, 1894, pp. 243-248; Heil, 1936, p. 10). Nevertheless, the present study showed that movement is the most important single element in the visual sign stimulus pattern, in both courtship and threat display, in all the salticids tested. Although display was occasionally obtained by a motionless spider, the courtship response always occurred under the following conditions: first, the stimulus was a female; second, the displaying male was of A-tone with exceptionally low threshold; third, the motionlessness of the stimulus was the only unusual factor in the situation. On other experimental occasions in which the above conditions were fulfilled, however, only negative responses were drawn. Table IV gives test data and results of pertinent experiments.

In many (certainly more than twenty) unrecorded, casual observations, a normal spider, which was sitting quietly when the male to be tested was introduced, would not draw a display until it moved, even though the two spiders were close together and the test male, judging by his actions—his turning, or moving toward the stimulus—had certainly become aware of the stimulus.

In more than 300 tests on 10 species, in which the stimulus was in some way unnatural, no positive response was ever obtained until the stimulus was moved. Many times the slightest, brief, manual twitching of the cardboard mount was enough of an

TABLE IV.

Responses of Males to Motionless Females.

*Series A.* Conditions. Male of A-tone; normal female chloroformed, placed on cardboard mount in approximately natural position; chemotaxis, but not distance chemoperception, eliminated (i.e., fresh sheet of paper on open table used for each test); same female in experimental session drew display from same male both before test (followed by rest) and immediately after. Exposure of each male to stimulus consisted in allowing him to drop near, or run toward, female, chivvying him gently with brush if necessary, to ensure her being in his direct line of vision. Even in negative responses, attention was often gained, even extending to feeling of the female with palps and legs, although display was not released.

| Species. | No. of Individuals. | No. of Tests. | Negative Responses. | Positive Responses. |
|---|---|---|---|---|
| *Menemerus bivittatus* | 5 | 7 | 6 | 1 |
| *Semorina brachychelyne* | 1 | 2 | 2 | 0 |
| *Sassacus flavicinctus* | 2 | 2 | 2 | 0 |
| *Phiale dybowskii* | 1 | 5 | 0 | 5 |
| *Phiale flammea* | 2 | 3 | 0 | 3 |
| *Corythalia chalcea* | 1 | 1 | 0 | 1 |
| *Corythalia xanthopa* | 4 | 12 | 11 | 1 (delayed) |
| Total | 16 | 32 | 21 | 11 |

*Series B. Chemotaxis permitted.* Conditions as in A, but males permitted to cross repeatedly trails of the now motionless females.

| Species. | No. of Individuals. | No. of Tests. | Negative Responses. | Positive Responses. |
|---|---|---|---|---|
| *Menemerus bivittatus* | 4 | 9 | 8 | 1 |
| *Sassacus flavicinctus* | 2 | 2 | 2 | 0 |
| *Corythalia xanthopa* | 4 | 8 | 8 | 0 |

*Series C. Elimination of Distance Chemoperception and Motion.* Conditions as in A, but female isolated in glass vial. No tests completed, since males did not display even when the stimulus female regained consciousness and moved naturally. However, in spite of the imperfect conclusions, it is worth recording that not one positive response was drawn in a total of more than 20 tests involving the same species listed in Series A. The enclosing of tested males, rather than stimulus females, would not have given significant results, since the effect of possible self-stimulation through crossing of their own tracks or responding to their own distance chemical stimuli, would not be eliminated. Similarly, mirror responses automatically involved sight of the males' own motions (however slight).

*Series D. Alteration of Female Appearance.* Conditions as in A, but female painted or upside-down. More than 25 tests, using stimuli which gave positive responses when moved, were all negative when motionless. See pp. 191 and 193 for tested species; all were given motion response tests in the same session. No stimulus which was unsuccessful when moved drew display when motionless.

*Series E. Use of Models.* No motionless model, even when successful in motion, drew a positive response. See p. 190. Test individuals were given motion-response tests in the same session.

addition to the stimulus situation to draw a prompt display.

This manual jerking of the mount of a chloroformed or fresh dead female was as effective as the female's own motions in drawing display. Her further motion was not essential, once the male had initiated display; it is, however, customary in normal courtship for even A-tone females to turn and twist and, especially, to retreat a few inches at least once or twice during courtship.

Also, the finer motions of females during male display almost certainly have value. In various species—in *C. xanthopa*, for example—females early in courtship brace themselves high in a position similar to a pre-threat stance in males. Just before *or* after the beginning of the male's Stage II, they crouch low. Again, in very many species, the females vibrate the palps rapidly during the early stages of courtship. Finally, in a few species, notably *C. fulgipedia* and *Sassacus ocellatus* among Rancho Grande examples, excited females often make weak copies of the males' motions, with occasional individual quirks of their own. None of these female motions ever proved to be in the least necessary either to release or to direct male display. There seems no question, however, but that they have minor directive value, and the female's eventual, crouching quiescence, as in other animal groups, certainly acts as a positive factor in permitting the continuation of Stage II. Also, it is this crucial point which in intermediate genera largely determines the continuation of display as Stage II courtship or as contact threat or actual fighting. In final summary, however, the function of female posture and motion changes is minor: in no genus which I have observed closely does the release of Stage II depend. in lock-and-key fashion, on any motion, or cessation of motion, in the female.

From the female's viewpoint, the sight of a male making appropriate courting motions is essential for acceptance. Exactly what constitutes, for each species "appropriate motion" is, however a completely unsolved question of obvious evolutionary interest. Since no method has yet been devised of testing this aspect, only the following general remarks may be made.

Little or no notice is taken of motionless males, although occasionally an A-tone female will approach or even touch one, without any attempt to injure or eat him (cf. behavior toward a partly blinded male, p. 185). No male was ever allowed to mate without complete courtship for the species, although sometimes the whole display was raced through in less than a minute, with no repetitions of stages, where both individuals were of high tone. In the occasional instances where males, because of low tone or a confusing experimental factor, omitted display and leapt directly on the female, she invariably drove him off or escaped.

Many males of high tone court females of similar-appearing or closely related species. These females are often attentive for long periods and make no effort to attack or retreat. It is usually the female that withdraws, often before Stage II is reached. It has yet to be determined how much her withdrawal depends on the, for her, "incorrect" pattern of male motion, and how much on the unsatisfactory character of other elements in the stimulus configuration.

In the release of inter-male threat display, motion is usually essential. Once a *C. xanthopa*, of especially high A-tone, did perform threat to a chloroformed male; this, however, was the only exception in more than 25 trials on different species. Those males which react to their mirror images will very rarely display unless the mirror is moved jerkily forward.

One more point should be emphasized in regard to motion in general. The positive responses to motionless stimuli, of whatever nature, usually occur when the test spider is dropped suddenly near the stimulus. It seems likely that the visual effect to the spider may be similar to that obtained when the stimulus is moving—roughly analogous to a human passenger's confusion when one of two parallel trains starts to move.

To sum up: Male display is sometimes released in the presence of motionless females. In these cases, however, the males are of extremely high epigamic tone (A-plus), the females of unaltered appearance, and the general external conditions propitious. Therefore, although movement of the stimulus is not a primary releaser for courtship, it is an important secondary releaser, and, doubtless, a director as well. Appropriate motion of the male is essential for acceptance by females. The response to motion does not appear to vary with the degree of specialization within the family.

iii. *Distance*. The distance at which salticids perceive their prey and mates, and at which they start display, has been measured for a variety of species (e.g. Peckham, 1894, p. 242; Homann, 1928, p. 247 ff.). In this study it is pertinent to add the following remarks and conclusions.

*Corythalia xanthopa*, which averages around 4.3 mm. in length, is typical of moderately small species at an advanced stage of visual evolution. Males will come to a state of attention and approach a female on the same level, from a maximum distance of ten inches, but the usual limit of attention (as distinct from display) is not more than six inches for courtship, much less for threat. Neither courtship nor threat usually takes place at more than three inches, and usually at 1.5 to two inches. At the resumption of an interrupted series, however, it may start at 3.5 to four inches. Stage II, in courtship or threat, starts at less than one inch, usually at about half an inch. *C. chalcea* and *fulgipedia*, which have apparently equal visual dependence with *xanthopa*, are both somewhat larger than the latter; in correlation

TABLE V.

Response of *C. xanthopa* Males to Spiders of Unusual Size.

*Conditions.* All tested males of A-tone, giving prompt response to one or more standard stimuli before and after test period; rules to avoid summation observed; all fed less than 24 hours previously; stimuli presented on open table, on same plane as tested spider; chemotaxis not permitted (fresh paper for each test, no trail crossing allowed.) Distance chemoperception not specially eliminated, although a short subsequent series of control experiments, with same stimuli dried and mounted, gave closely similar results; in other experiments (pp. 177 ff.) it was established that A-tone males react with threat display as fast or faster to mirror images and mounted dried *xanthopa* males, when manually jerked, as to naturally moving males. Stimuli were lightly chloroformed and placed on mount, which was moved jerkily in front of tested males and/or allowed to move naturally as effects of chloroform disappeared. Stimuli were reinforced by being chivvied constantly in front of tested spider, as necessary. When no response occurred within three minutes, results were counted as negative.

*Supplementary Data Concerning Table. "Approx. proportion xanthopa visible area"* (second column), roughly indicates size of stimulus, in an alert, semi-resting position (except in the display-mounted *chalcea*) in comparison with that of *C. xanthopa*, from a direct frontal view. The proportions were taken by multiplying the height (ground to top of carapace) by the distance between the most laterally directed tarsi.

In the large *Eustiromastix* sp., the largest local salticid, the male in frontal view is unadorned black, the female dark brown with many gray and white hairs. A tendency was shown in positive responses to react with display at more than normal distances to these large stimuli.

The small *Corythalia* sp., not yet described, were brought alive to Rancho Grande from Caracas for the experiments; the clypeus has a small, creamy white spot; legs black with faint white spots.

Obviously, the data in this table are connected with responses to form, pattern and color.

| Name | Remarks. | Approximate proportion *xanthopa* visible area. | Number tested. | Number of tests. | Responses. | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | Threat. | Courtship. | Mixed, threat-courtship. | Fear-flight behavior. | Stalking-crouch behavior. | Attention only or no reaction. |
| A. Stimuli larger than *xanthopa*: | | | | | | | | | | |
| C. *chalcea*, ♂ | normal | x 1.65 | 10 | 20 | | | | | | 20 |
| C. *chalcea*, ♂ | clypeus painted yellow | x 1.65 | 9 | 10 | | 2 | 1 | 4 | | 3 |
| C. *chalcea*, ♂ | normal, mounted in threat position | x 2.5 | 1 | 2 | 2 | | | | | |
| C. *chalcea*, ♀ | normal | x 2.5 | 2 | 2 | | | | 2 | | |
| *Eustiromastix* sp., ♂ | clypeus painted yellow | x 4.8 | 6 | 10 | 8 | | | | | 2 |
| *Eustiromastix* sp., ♀ | normal | x 6.0 | 4 | 4 | | | | 2 | | 2 |
| *Eustiromastix* sp., ♀ | clypeus painted yellow | x 6.0 | 3 | 6 | | | | 5 | | 1 |
| Large heteropodid ♀ | clypeus painted yellow | x20.0 | 5 | 10 | | | | | | 10 |
| B. Stimuli smaller than *xanthopa*: | | | | | | | | | | |
| *C. xanthopa*, pre-pre-adult | clypeus painted yellow | x 0.2 | 5 | 5 | | | | | 2 | 3 |
| *Corythalia* sp. ♂ | normal cream-spotted clypeus | x 0.3 | 6 | 8 | 2 | 2 | | | | 4 |
| *Corythalia* sp. ♂ | clypeus painted yellow | x 0.3 | 3 | 3 | 1 | 1 | 1 | | | |
| C. *xanthopa*, ♂, pre-adult | normal (sparse clypeal yellow) | x 0.6 | 5 | 5 | | 2 | | | | 3 |

## TABLE VI.

### Spectral Reflectance of Paints Used in Salticid Experiments.

Conditions: Ultraviolet (UV) reflectance judged optically from comparative inspection of negative images of paint samples; lens, Leitz 50 mm. Summar; film, Eastman Super XX; filter, Wratten No. 18A; exposure, 1 sec. @ F 3.5; illumination, light from north sky, partly cloudy, noon, June, latitude 10° 21′ north. Spectral reflectance readings from curves furnished by Electrical Testing Laboratories, N. Y., made from same samples on Hardy spectrophotometer; reflectance factor in terms of magnesium oxide.

| Wave-length (mμ) | Reflectance Factor | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | White (Devoe) | Blue (Devoe) | Green (Devoe) | Yellow-green (Devoe) | Yellow (Devoe) | Yellow (Flo-quil) | Orange (Devoe) | Red (Devoe) | Red (Flo-quil) | Red-&-white (Devoe) (Pink) | Black (Devoe) |
| UV | very strong | strong | weak | very weak | very weak | very weak | very weak | weak | very weak | strong | very weak |
| 400 | .715 | .432 | .080 | .067 | .115 | .067 | .050 | .080 | .030 | .450 | .025 |
| 410 | .725 | .450 | .082 | .070 | .120 | .067 | .055 | .087 | .032 | .462 | .032 |
| 420 | .735 | .480 | .090 | .075 | .130 | .067 | .057 | .092 | .033 | .477 | .035 |
| 430 | .750 | .515 | .095 | .082 | .145 | .067 | .058 | .095 | .035 | .492 | .035 |
| 440 | .755 | .535 | .110 | .090 | .165 | .068 | .060 | .098 | .035 | .512 | .035 |
| 450 | .765 | .550 | .135 | .107 | .197 | .070 | .063 | .013 | .035 | .522 | .035 |
| 460 | .770 | .545 | .180 | .145 | .250 | .070 | .065 | .012 | .037 | .520 | .035 |
| 470 | .775 | .505 | .255 | .215 | .330 | .075 | .067 | .095 | .038 | .518 | .035 |
| 480 | .780 | .440 | .365 | .345 | .425 | .078 | .068 | .087 | .040 | .513 | .035 |
| 490 | .782 | .365 | .475 | .475 | .520 | .087 | .072 | .085 | .043 | .507 | .036 |
| 500 | .785 | .280 | .545 | .565 | .597 | .105 | .075 | .077 | .045 | .498 | .037 |
| 510 | .785 | .215 | .552 | .617 | .640 | .157 | .077 | .072 | .052 | .492 | .037 |
| 520 | .787 | .160 | .520 | .637 | .667 | .265 | .080 | .068 | .057 | .488 | .037 |
| 530 | .787 | .125 | .470 | .637 | .680 | .402 | .083 | .070 | .060 | .493 | .037 |
| 540 | .790 | .097 | .405 | .620 | .685 | .515 | .105 | .070 | .062 | .502 | .037 |
| 550 | .790 | .080 | .335 | .592 | .692 | .575 | .160 | .067 | .067 | .507 | .038 |
| 560 | .792 | .067 | .275 | .560 | .697 | .615 | .270 | .068 | .075 | .510 | .038 |
| 570 | .795 | .060 | .220 | .535 | .700 | .640 | .420 | .075 | .080 | .530 | .038 |
| 580 | .800 | .057 | .185 | .525 | .705 | .657 | .550 | .100 | .085 | .580 | .039 |
| 590 | .805 | .055 | .167 | .523 | .713 | .670 | .625 | .180 | .115 | .650 | .040 |
| 600 | .810 | .057 | .155 | .525 | .715 | .677 | .665 | .335 | .195 | .715 | .040 |
| 610 | .812 | .060 | .147 | .532 | .725 | .678 | .688 | .550 | .310 | .747 | .040 |
| 620 | .817 | .062 | .137 | .550 | .737 | .678 | .705 | .575 | .395 | .755 | .040 |
| 630 | .820 | .067 | .132 | .577 | .747 | .678 | .718 | .625 | .450 | .777 | .040 |
| 640 | .825 | .080 | .135 | .615 | .752 | .677 | .735 | .657 | .478 | .787 | .040 |
| 650 | .830 | .092 | .145 | .640 | .763 | .677 | .750 | .680 | .493 | .798 | .040 |
| 660 | .835 | .115 | .167 | .657 | .777 | .678 | .765 | .700 | .502 | .807 | .041 |
| 670 | .845 | .145 | .195 | .665 | .790 | .680 | .780 | .722 | .510 | .818 | .041 |
| 680 | .850 | .190 | .225 | .657 | .795 | .683 | .792 | .740 | .513 | .827 | .042 |
| 690 | .855 | .242 | .280 | .653 | .805 | .685 | .802 | .755 | .522 | .838 | .042 |
| 700 | .860 | .315 | .342 | .663 | .815 | .688 | .813 | .767 | .527 | .843 | .043 |
| 710 | .863 | .392 | .407 | .692 | .820 | .690 | .820 | .773 | .532 | .850 | .043 |
| 720 | .865 | .465 | .463 | .720 | .823 | .693 | .827 | .787 | .535 | .853 | .042 |
| 730 | .867 | .530 | .515 | .745 | .827 | .697 | .832 | .795 | .538 | .858 | .042 |
| 740 | .870 | .577 | .558 | .770 | .830 | .698 | .835 | .780 | .540 | .860 | .042 |
| 750 | .872 | .610 | .595 | .790 | .834 | .702 | .840 | .887 | .542 | .862 | .042 |

they have slightly greater attention and display limits, thus illustrating a general principle of the spatial limits of salticid responses.

In comparison with *Corythalia*, species which still place a relatively high dependence on chemotaxis and/or distance chemoperception, appear relatively short-sighted. Thus, *Ashtabula* and *Semorina*, although similar in length to *C. xanthopa*, rarely give evidence of first attention at more than four inches, and usually much less. Display begins even closer, and, as always, Stage II starts closer than Stage I.

It must be kept in mind that two spiders are seldom in the same plane in the field; therefore, one customarily enjoys the advantage of an obliquely downward view on the expansive dorsal surface of the other.

Once more the importance of the physiological state should be emphasized: A-tone males tend to start attention and display responses at greater distances than others.

iv. *Size*. The display responses of salticid males to stimuli of unusually large and small size do not appear to have been previously investigated. In this study *C. xanthopa* was subjected to a series of experiments, the

distinctness of its threat and courtship responses making it an especially interesting species. Because of the importance of distance chemoperception in its courtship releasing mechanism, males rather than females were usually selected as stimuli. The results of the tests appear in Table V. In casual observations on other species, primarily concerned with inter-specific display, it was always true that where two species had display relations, there was never much discrepancy in size.

Conclusions: First, Appropriate size is an important secondary sign stimulus to display. No male *xanthopa* will give any kind of a positive display reaction to a spider with a frontal area of more than five times, or less than one-third, of his own. In other words, in linear measurements, positive responses may be given to stimuli measuring up to about twice natural size and down to about one-half.

Second. The responses within this range are highly variable and signs of confusion are frequent. The courtship response is often given in these unusual size ranges to stimuli to which a threat response would seem more appropriate.

Third. Addition of a clypeal band of yellow paint to an otherwise black frontal view, sometimes changed negative to positive responses. This yellow resembled, to human vision, that of *xanthopa* males. Both brands used had slight reflectance below about 520 mμ (Table VI).

Fourth. As usual with unnatural stimuli, responses were usually obtained only by deliberately reinforcing the stimuli. This was accomplished by repeated presentations in quick succession, and constant chivvying to keep them moving in the direct front visual field of the spider. Spiders below A-tone gave consistently negative results.

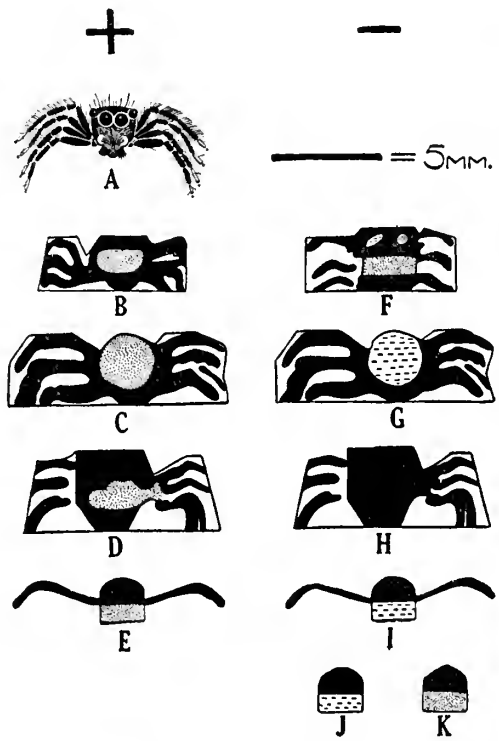
Fifth. There was a tendency to respond to large stimuli at longer range than the normal.

v. *Form.* The general shape of the spider is another secondary sign stimulus for releasing display. Heil (1936), working with life-size pictures of *Evarcha*, performed some experiments on this subject. He found that the number of positive display responses decreased rapidly with the simplification of the drawing, particularly in the reduction of lines representing the legs. The following results, which support and extend those of Heil, were obtained at Rancho Grande.

As in other factors, the importance of form varies inversely with the normality of the test situation, and with the drive of the individual; an A-tone *C. xanthopa* of especially strong drive will respond (with threat) to a jerked, life-size paper model of great simplicity, to the jerked carapace of a dried male, or to a jerked or naturally moving normal male with a high black paper "hat." None of these extremes is successful under other conditions, or in combination with one another. For example, none of them draws display from a male of mediocre drive, while a legless paper model or a motionless carapace is unsuccessful even with males of the highest tone.

Because of the variety of contributing factors, a tabular representation of the experiments in this series would not give as true a synopsis of the results as the following running account with selected and annotated field notes. All of the experiments were performed under the conditions described under Table VI. In this series the tested species were *Corythalia xanthopa*, *C. chalcea* and *Phiale flammea*, all visually advanced species in which chemotaxis and distance chemoperception are of reduced importance.

*Models.* Cardboard models were tested on male *C. xanthopa*. Drawings of successful and unsuccessful models, made through a binocular microscope, are shown in Text-fig. 7. "A" represents a careful drawing of a male in threat position, for comparison, and was not used as a model; such detail, would, of course, have been impossible to include on a




TEXT-FIG. 7. Examples of models used in experiments on form-pattern-color perception in *Corythalia xanthopa*. The stippled areas were painted yellow, the dashed areas white, the backgrounds light green; spectrophotometric data in Table VI. **A**, detailed drawing of *C. xanthopa* in threat position; **B-E**, drawings of pasteboard models which drew threat responses, in order of their success, from the most (B) to the least (E); **F-J**, unsuccessful models. Note that the only difference between successful and unsuccessful in some cases was the presence or absence of a yellow median area. See text.

surface 5 mm. across. Similar models, but relatively larger or smaller than those shown were never successful. Even the unsuccessful models (right column) drew some attention from A-tone males. All were drawn in Higgins India Ink on bits of pasteboard; interstices between "legs" were painted pale green (see wave length analysis, p. 189 for this and other colors mentioned hereafter), from the same jar as the mounts and similar in reflectance curve to the paper substratum. This tint, used frequently as background in series of experiments involving living stimuli, appeared, from the tested spiders' behavior, to provide for them excellent contrast.

The most successful model was B, the least successful in the positive series, E. The best of them, however, drew only delayed display. It will be noted that all successful models had the following characteristics: a roughly squared or rounded central portion, painted matte black and yellow, with a greater or lesser series of lateral extensions. The "eyed" model (F) was never successful, nor were models similar to or identical with the successful one except for black or white in place of yellow in the central region. Plain black quadrilaterals—i.e., without "legs," but covering the same area as B and D—were always unsuccessful, even when furnished with a median yellow spot or bar. Also unsuccessful were all more extreme models, including equilateral and isosceles triangles; the latter were tried both vertically and horizontally, and all were furnished with a median yellow area. Finally, no small, median portion, representing the carapace only, ever drew a response.

*Form Experiments with Specimens.*

*General Shape.* The following experiments also show the necessity for a general shape approaching the normal. A young adult female *C. chalcea* was lightly chloroformed, placed on an L-mount and covered with a bit of flimsy black silk (chiffon), which scarcely enlarged her, but effectively concealed her shape. When she was jerked before a high tone male, no display was drawn. However, when the whole was surmounted by a large, dried *Eustiromastix* sp. (a male, plain dark brown with a painted yellow clypeus), the *chalcea* promptly courted, following through to attempted mating—not with the hidden *chalcea*, but with the *Eustiromastix*. Single, fresh abdomens, of both males and young females, were presented to males of *xanthopa, chalcea* and *P. flammea;* none ever drew display, or even attention, from a total of about 25 tests. Detached fresh legs, singly or in groups, were equally ineffective.

*Importance of Legs.* A legless, dried male *xanthopa* cephalothorax was very rarely successful in drawing threat display. Similarly, a legless and palpless young female *chalcea* (but with abdomen intact) drew delayed display in only three of nine tested males. However, none of these positive responses was complete: one male broke off display and jumped, several times in succession, at the female; another, after a delayed Stage I, merely climbed onto the cardboard mount beside her, palpating its surface; a third reached Stage II, but did not follow through to twisting the abdomen, his display dying out in palpation of her body and the surrounding mount.

A single real leg was then laid flat at each side of the female, without drawing a response; but when two pairs were used, delayed but complete courtship followed.

When a sling of stiff black cotton, shaped like a broad, inverted W, was substituted for real legs, brief and abortive display followed. When a second sling was added, so that the front view showed lateral stripes of alternating light and dark, prompt, complete courtship ensued. When the second sling was removed, there was once more no response, which however followed promptly upon the second sling's replacement.

Throughout all the experiments with *xanthopa,* it proved axiomatic that mounted dried or chloroformed males with the legs stretched out at the sides drew threat display from males of mediocre drive faster than those in a huddled position.

Upsidedown females of *xanthopa, chalcea* and *P. flammea* were tested. These almost never drew display, the rare exceptions being from males of the very highest tone. The display never started until abnormally close to the stimulus and Stage I was exceptionally brief; occasionally a male would approach a female without display, palpating her for a time before wandering off. No actual mating attempts, which were always preceded by some display, were ever successful, the males groping about in evident confusion. Upsidedown males, on the other hand, never drew threat display or, in fact, more than passing attention.

*Importance of Carapace Height.* Compared with the legs, the height of the carapace is of very minor importance. Its elevation off the ground has no perceptible significance, judging from the prompt response of male *xanthopa* to the various mounts and of other forms, including *Menemerus, Sassacus, C. chalcea* and *Phiale,* to various dried or chloroformed mounted examples of their own species, none of which was ever presented balanced in life-like fashion on the legs. It must be remembered, however, that in normal display one of the most usual factors is the elevation of the carapace high on the legs.

Black and white paper "hats" of various sizes and shapes were fastened above the eyes to males and females of *C. chalcea* and *P. flammea* with rubber cement. So long as other conditions approached the normal, appropriate display was delayed little or not at all, and a female *chalcea* readily accepted a black-hatted male. However, in the case of hatted females, the males did not carry display through to actual mating attempts, in

this small set of "hat" tests which totalled about a dozen. The highest addition tried measured twice the height of the clypeus-plus-AME-diameter.

*Conclusions.* First, shape is of secondary significance in the release and direction of display.

Second, deviations in shape which do not hinder display release nevertheless often prevent mating.

Third, the primary shape requisite for releasing and directing either courtship or threat in *Corythalia* and *Phiale* are a roughly quadrilateral figure, broader than high, the lateral portions of which show some suggestion of dark and light horizontal stripes.

Fourth, the vertical dimension is less important than the horizontal as a factor in display.

Fifth, when the shape of a stimulus deviates from the normal range of variation, the tested spider must be of high tone and the other factors in the display situation must in general be normal, in order to draw a display response.

vi. *Pattern, Intensity and Color.* The parts played by pattern, intensity and color in courtship and threat displays are, as in other groups, exceedingly difficult to determine and to distinguish; in the present study only the surface of the question has been scratched. It should be pointed out that the distinction made here between "shape" and "pattern" is obviously artificial, although, in the preceding section on shape the emphasis was on the general form of the figure, rather than on the details; however, the stimulus value of the legs certainly belongs as much under "pattern" as under "shape."

The Peckhams (1887, p. 403) were the pioneers, as usual, in investigating color perception in spiders. Working altogether with lycosids, they approached the problem through a choice method, the lid of the cage being covered with glass squares differing in color. Since neither intensity nor wavelength was controlled, their results can have no final significance for modern workers. Nevertheless, it is very suggestive that the vast majority of *Lycosa* chose "red," since these spiders are largely negatively phototropic; very likely the hunting spiders in general, like the majority of insects, will prove to be relatively insensitive to the red end of the spectrum.

The Peckhams performed another series of experiments, painting female salticids partially or completely "blue." Following painting, the previously displaying males paid them much less attention, either not displaying or delaying the response, although it was resumed promptly when normal females were introduced. A number of uncontrolled factors were of course involved in this series (1894, p. 249).

Kaestner (1949) has just published a preliminary report indicating that color perception does occur in the European genus *Evarcha.*

Apart from the question of actual color perception in salticids, the minor role played by color, or at least by lightness and darkness, in courtship is shown by *Maevia vittata,* the North American salticid with dimorphic males. Painter (1913) seems to have been the most recent worker on the subject. The dimorphism is controlled by the presence or absence of a small sex chromosome, and in the population studied the two forms were about equally abundant. The principal distinctions consist of general color—black in one, gray with orange palps in the other—and the presence of a pair of tufts on the carapace in one, absent in the other. In spite of considerable individual variation, the two forms are quite distinct visually; in addition, the display patterns show differences. Nevertheless, both were readily accepted by females, as were dark males with their tufts missing. According to the Peckhams (1889, p. 54), who worked in a different part of the United States, the darker, tufted form was more aggressive, and was preferred by the females; also, differences in display of the gray form from that described by the Peckhams were reported by Painter. In spite of the fact that in neither study were controlled experiments performed, which guarded against summation, etc., it still seems likely that a most interesting series of behavior differences has evolved in this widespread species. Here is certainly splendid material for worthwhile work.

The disagreements between the Peckhams and Painter do not affect the conclusion that degree of lightness or darkness in males is not, in that species, of primary importance in gaining acceptance by the female.

In the present experiments, two groups of colors were used, the Floquil "Flo-paque" series and Devoe opaque water colors. Since spectrographic analysis could not be conducted in the field, library cards were painted with each hue and combination used; later these were analysed spectrophotometrically (Table VI), along with fresh samples from new jars. The latter check was employed to determine the degree of changes in the samples since their field use; these differences proved insignificant. Although the paints are far from a theoretical monochromatism, most of the hues do show steeply ascending curves near the regions of highest reflectance.

During the field experiments, the paints and the yellow of *C. xanthopa* (cut in two, without exposure to chemicals, just before the photograph was made) were photographed through Wratten Filter No. 18A, which screens out virtually all light except the ultraviolet; the spider's yellow areas did not perceptibly affect the negative according to observations through a binocular microscope. (Spider photographic data: lens, Leitz 90 mm. Ektar; exposure, 13 sec. @ F12.7; other data as in Table VI). In view of these

negative results, it is apparent that ultraviolet is not a factor in the effect of *xanthopa* yellow as a sign stimulus; they do not of course, preclude the possibility of the spider's visual sensitivity to ultraviolet wave-lengths. So far the yellow of the spiders has not been further analyzed: dried specimens appear to be too changed to give trustworthy results.

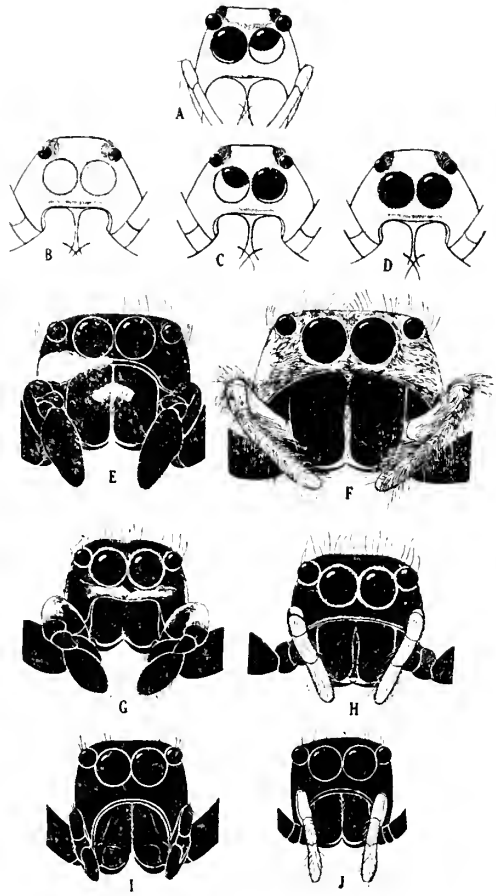
It will now be shown that the various characteristic "display ornaments" are in themselves of minor importance in the samples studied as display sign stimuli, except in certain inter-male relationships. *C. xanthopa* was the subject of most of the experiments; *C. chalcea, C. fulgipedia, Menemerus bivittatus, Phiale flammea* and *P. dybowskii* were used to a lesser extent; a few illustrations were taken from *Semorina, Ashtabula* and *Sassacus.*

*The Role of Female Pattern, Intensity and Color in Stimulating Male Display.* The female's pattern and color equipment may be divided between that of the frontal and the dorsal (particularly abdominal) regions. It must be kept always in mind, however, that in practice the male's first view of the female is often obliquely downward, so that both regions are simultaneously visible. In the experiments below, the two regions were kept separate, the stimuli being presented on a plane surface in direct frontal or rear views.

*Frontal pattern.* (Text-fig. 8). In females, this may be divided functionally into two well-marked classes; first, differentiation of frontal markings, including those of clypeus and palps as a unit, and, second, distinctions concerning the palps alone. The sexual difference of frontal markings is noticeable in many salticids, but ranges through all degrees and is often absent. The following examples are from the present series: In *C. xanthopa* and *Phiale* spp., the females are black-faced while the males have strong yellow or white clypeal bands which continue, when the palps are bent, onto certain palpal segments. In contrast, in *C. chalcea, C. fulgipedia* and *Eustiromastix* sp., the females are frontally moderately or very hairy, chiefly gray and white, while the males are almost completely black and naked. In *Menemerus bivittatus,* both sexes have the hairs pale, but the female more so than the male, where they are confined to a white clypeal band. Finally, in *Mago acutidens,* the frontal region is black and naked in both sexes. It should be remembered that the legs, particularly the first, are often much darker in males than in females.

Experiments were made with *C. xanthopa* and *P. flammea,* both having sexual dimorphism in this respect, to determine the effect on the male of alteration of the clypeus.

When normally black-faced young female *xanthopa* were given yellow clypei and palpi, resembling those of the male, the courtship display was always drawn as promptly as ever with no hint of threat or confusion. Chemotaxis, but not motion or distance chem-




TEXT-FIG. 8. Examples of frontal sexual dimorphism and types of "ornamentation" in representative salticid genera. **A**, *Lyssomanes bradyspilus,* female; **B**, **C**, **D**, same, male, showing three positions of ocular color "change"; **E**, *Menemerus bivittatus,* male; **F**, same, female; in the male, one-half of the white clypeal band has been shaved off to show narrowness of true clypeus; **G**, *Phiale flammea,* male; **H**, same female; **I**, *Mago dentichelis,* male; **J**, same, female. All figures drawn to same scale; note how in *Mago* the individual female depicted happens to be smaller than the male; this often occurs in salticids, although the carapace size of the average female in a given species is always somewhat larger than that of the average male.

The adaptive value of the "ornamentation" is by no means equal throughout the family. In *Phiale,* the clypeal band of the male is a releaser for threat display; in *Menemerus* there seems normally to be no inter-male display at all, although a similar clypeal band is well developed, nor is it of apparent importance in courtship; *Mago,* lacking all clypeal "ornamentation", but having a plain, high, black carapace and clypeus, has both courtship and threat well developed and moderately well differentiated. Note the prevalence of pale palps in the female; these are usually vibrated during display, but do not, in the several tested genera, function as either primary or secondary releasers of male courtship. Sexual dimorphism varies from negligible (e.g., *Mago*) to extreme (e.g., *Menemerus*); see also Part I, 1948.1, text-figs. 12-15 incl., for examples of the latitude of dimorphism within a single genus, *Corythalia.*

ical stimuli, was excluded. (Test-material: 2 females, 6 males, 9 tests).

Four weeks later, one of the same females, still unmated, but now more than "middle-aged" for that species, was given a new coat of paint and presented to a fresh series of males. The results were quite different: (Test-material: 1 female, 7 males, of which 6 were of A-tone and 1 of B-tone; 10 tests.) First round: 2 threat, 3 courtship, 2 undecided; second round (3 only tested): 1 threat (last time this individual was uncertain), 1 courtship (last time this individual also courted), 1 courtship (last time this individual was uncertain). Total of responses: 3 threats, 5 delayed courtships, 2 confused responses (including that given by the low-tone individual). The threat reactions were all promptly given, while courtship followed a period of uncertainty characterized by attention, "following" with the eyes, and intermittently dropping the abdomen (i.e., alternating in courting and threat position). It seems apparent, in conjunction with other experiments, that the waning airborne chemical stimuli of the female were here responsible for the inclusion of threat and uncertainty in the results.

Two male *xanthopa* were now altered; in one the yellow scale-hairs of clypeus and palps were painted black; in the other the palps were detached and the clypeal scales scraped off with a razor. The results (5 males tested, 5 tests) consisted of 2 very rudimentary brief courtships (1 single rock each), 1 abortive, brief, courtship-plus-threat and 2 responses which were negative except for brief attention. When a mirror was presented to the palpless, shaved male, as he stood on the same spot where a young female had just been sitting, he gave prompt attention, courtship stance and a few rocks, then retreated briefly, and ended by leaping at the mirror, but above the image level. The same response was repeated on fresh paper, but since no rest time was given in this instance, summation may well have been involved; unfortunately because of an accident to the shaved male, and lack of time for repetition, the testing was not resumed.

When similar experiments were conducted on *Phiale*, the results were as follows:

When a normally black-faced young *P. dybowskii* female was given white spots on the palps and, later, a white clypeal band similar to those of the males, repeated tests always drew complete courtship, not threat.

When an old *P. flammea* female was similarly treated, two males courted relatively promptly so long as she was motionless, but approached her, for mating, from the side, out of sight of the abnormal, white palps and never got properly oriented toward the abdomen.

When the female mount was moved during the presentation, the male first gave threat, changing to a prolonged, side-approach courtship only when he was unusually close to her. When her paint was washed off, both males gave prompt, normal, complete courtships.

The entire frontal aspect of a young chloroformed *C. chalcea* female, excepting the eyes, was painted white. As she sat motionless on a mount, an A-tone male was introduced with the following results: "He soon vibrated palps in the air, making semi-circles until he came close to the mount. Then he palpated and further vibrated the palps, circling off on the surrounding paper and returning to mount time and again. However, there was no trace of display, and no attempt to mate. It was exactly like the behavior of a male introduced to the spot where a female had recently been sitting or moving about. Finally, after more than five minutes, he went away. When he was brought back, to a distance of about two inches, the female was jiggled infinitesimally. He displayed at once, with good courtship. The first mating attempts in Stage II were from her unpainted rear. Then he displayed Stage I again and approached with a typical Stage II from the front." (Field lab. note).

One typical feature of the female frontal appearance in many species is the rapid vibration of contrastingly pale palps at a certain stage of courtship; it occurs usually in the earlier phases, during her first apparent awareness of the male's Stage I. Sometimes, as in *Semorina*, *Ashtabula*, *Phiale* and *Mago*, contrast to the otherwise dark front (including or excluding legs), is attained principally through pale integument; sometimes, as in *Menemerus*, the effect is accentuated by long white fringes. In species such as *C. chalcea*, where vibration of the palps by the female is of casual and infrequent occurrence, they are not notably lightened or "ornamented." When present, the paleness and "ornamentation" usually extends to most segments, unlike special spotting with scale-hairs of certain segments which is so typical of some males, as in *C. xanthopa* and *Phiale*.

In order to determine their importance as display sign stimuli, the female's palps were removed from examples of *Menemerus* and *Phiale*. In every case the males courted the mutilated females as readily as normal forms. (*Menemerus*: 1 female, 8 males, 10 tests; *P. dybowskii*: 1 female, 1 male, 2 tests.) Palps were not removed from any of the other species, but males of all genera mentioned in the preceding paragraph always displayed as readily to a chloroformed female when her mount was slightly twitched as to a normally moving individual; the separate motion of contrasting palps is certainly not even a secondary sign stimulus.

In most females, as in males, the eyes are rimmed more or less conspicuously with reddish, yellowish or white scales. Since males display as readily to clumsily blinded females, in which all trace of the scales is covered, as to normal ones, these scales seem to have no primary or secondary display value in modern times.

*Dorsal pattern:* Dorsal carapace markings are almost always absent in the species studied, except in *C. fulgipedia* and *Phiale*, where they are highly variable and practically identical with those of the male; the white submarginal carapace bands characteristic of many species do not appear to be displayed in any of the ones I have observed and, indeed, short of a theoretical lateral display, involving flattening of the legs, it is difficult to see how they would ever be plainly visible.

The females of *C. xanthopa* have a naked black carapace, but a prominent abdominal pattern, consisting of a pair of broad, longitudinal, yellow stripes on a black ground. Males frequently display to the rear view of normal females before they have seen her dark front view at all. Blackening of the female abdomen produced no change in reaction time (1 female, 2 males, 6 tests). Then two young females were selected, of similar age and condition; the abdomen of one was blackened; they were then placed, facing away from the center, about eight inches apart on the ten-inch line of the concentric test circles (Part II, 1948.2, p. 145), this being about the limit of perception-response in this species. Six males in A-state were then placed in succession in the circle's center, facing exactly between the two females. In every case the male became first aware (as judged by his shifting position to look toward her, and the adoption of preliminary courtship stance) of the female whose mount was twitched first, no matter how slightly. His progress toward her was invariably interrupted by a movement from the other female, regardless of her color. By the time the male arrived within actual courting distance (several inches away), he would either court first one, then the other, impartially, or simply sit, restlessly, between them in apparent confusion. In all, four of the six males courted somewhat, and two sat quiet at courting distance and eventually retreated. Of the courters, two eventually stopped and ran between the females out of range, one retreated, and the fourth's test was broken up when the normal female came out of the chloroform and moved off. At that point the male made no attempt to follow, but concentrated at once on the black female nearby, now not being twitched, and followed through into advanced Stage II before they were forcibly separated. A second round of tests, using the same males, brought similar results, although a given male did not always behave in the second test as in the first. The overwhelming effect in all tests was uncertainty and conflict. The only possible difference noted in the response to the two females was a very slight tendency to notice the normal female first at the greatest distance (10 inches), when both were twitched simultaneously.

Thus, although the female's pattern certainly has no value as a releasing stimulus, it seems likely that in the long run the two light stripes may have some slight directive value in the field. Under those natural conditions, three-dimensional vision is of course the rule. Therefore, the striking contrasts may make the attraction of the male's attention from farther than 10 inches, beyond the range of distance chemoperception, easier, among the dead leaves and shadows. To human vision, both males and females of this species are conspicuous in their normal habitat. However, I have never been able to gather the least evidence of this possible function, although it has been kept constantly in mind in field observations. In regard to *C. fulgipedia* females, which exhibit an abdominal pattern and color striking enough with their strong black and white, there are no distinctions from either immature specimens of almost equal size or from those of adult males; therefore the adaptive nature of abdominal pattern in any fashion, except that perhaps of disruptive coloration, is even more unlikely.

In female *chalcea*, any adaptation to display use is the most questionable of all; its dull bronzes, pale gold and black bandings are not only indistinguishable without a microscope from those of the preadult female, but they merge exceedingly well into dead-leaf or tree-trunk backgrounds, and when the spider moves it is even less conspicuous than an all-black form. If the color and pattern have any adaptive significance, it would appear to be as disruptive coloration of a protective nature; certainly it cannot help in attracting the attention of the male. A further point is that *chalcea* and *fulgipedia* females, although of strikingly different appearance, each draws display from males of the alternate species even when the males have only a posterior view.

When the abdomens of *xanthopa* females were painted solidly yellow to resemble those of males, there was no confusion: as when the clypeus and palps were painted, the male courted from the rear if the female was a young adult; as in the case of the altered front view, he became confused with old painted females.

In *Phiale*, the quite constant flaming rusty red of many species in the male is variable in females, ranging from almost male vividness to nearly black. The white spots and bars, though also variable, are nevertheless always present and, to human eyes, conspicuous, especially posteriorly. However, when the female abdomen was painted uniformly black in P. *flammea*, three males courted her promptly from the rear at close range. Nevertheless, in this genus pursuit is a fundamental, normal part of the courtship, and as often as not the male is displaying for a time to the female's posterior view. It seems therefore that while female white posterior markings have no releasing value, they, like the *xanthopa* stripes, are probably directive in the sense that they facilitate following.

In perhaps a majority of genera, the abdominal pattern appears completely undistinguished, except as probable examples of protective coloration. In *Sassacus ocellatus*, one of the species in which the female abdomen is both striking and closely similar to that of the male—i.e. iridescent green with posterior black-and-white spots—it is noteworthy that abortive female display was once observed (Part III, 1949, p. 46).

There is, however, one female abdominal marking which appears of importance in courtship. This is the sub-basal pale band, usually white, which is of such frequent occurrence in both sexes throughout the family. It is found even more often in females than in males. It is present in all of the adult females discussed in the present paper except *Lyssomanes*, *Semorina*, *Ashtabula* and *Corythalia xanthopa*. It always crosses the highest point of the abdomen and is preceded only by the naked black region immediately behind the pedicel.

In order to test its display value, abdomens were variously covered with white, yellow, black or red paint in females of *C. xanthopa*, *C. chalcea* and *P. flammea*. In painted *xanthopa*, in which the abdomen is normally striped, display proceeded though normal mating, as described earlier. In the other two species, which normally have sub-basal bands, the males appeared to become confused in the middle of Stage II, when the time came for twisting the abdomen. The following instance is typical: A *chalcea* female was painted completely white above, except for the thoracic slope of the carapace, which was inadvertently left black. Three males in seven tests courted normally until advanced Stage II, whereupon all of them tried to twist the carapace, not the abdomen, and made fumbling efforts to insert the palp too far forward. All of them gave up and moved off. When black paint was applied to this area also, lest the behavior difference involve negative chemical or other stimuli from paint, the same reaction followed. Finally, the base of the abdomen was blackened, the crest and all posterior to it remaining white. The two males still in display condition now promptly started mating after normal courtship, in the typical position. Cases of similar confusion occurred in *Phiale*: When the female abdomen was completely blackened, the males did not locate the epigynum; when a sub-basal white band was added in the usual position, courtship was completed without delay. (1 female; 3 males; 3 tests). The confusion following lateral approach in response to legless females has already been discussed (p. 191).

The following interim summary may now be made in regard to the role of female pattern and color in stimulating male display:

First. They are of the most minor importance, in comparison with other stimulus situation components, having no releasing functions and only rarely a directive value.

Second. Young adult females in the tested species, when painted to resemble males, or when the typical pattern is severely altered, are nevertheless courted as females, so long as the remainder of the stimulus configuration remains normal; otherwise there is no response.

Third. Old females so painted, or males painted to resemble females, draw delayed or confused responses, or, sometimes, complete threat display.

Fourth. The correlation of palp ornamentation and vibration in females, although it may well increase visibility to and/or excitement in the male, is certainly not even of secondary releasing value; males court palpless females of *Menemerus* and *Phiale*, as well as chloroformed—and hence quiet-palped—females of these and other genera, promptly and completely.

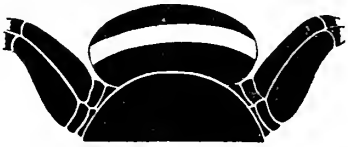
Fifth. While the white posterior markings or other patterns of some females may increase visibility to pursuing males, this is pure speculation; the markings are not necessary to release display, nor are any of the other tested female abdominal patterns.

Sixth. The white sub-basal abdominal band, which occurs so frequently in the family, proves to be a directing mechanism for copulation in *Corythalia chalcea* and *Phiale flammea*, the only two species tested. There is contributory evidence that this is also true in other species.

*The Role of Male Pattern and Color in Gaining Acceptance by the Female*: The following paragraphs summarize the experiments in this series. The difficulty in assembling data was in bringing treated males back to full A-tone display condition after the operation, and in having receptive females on hand at the right time.

*Menemerus bivittatus*. Five females all paid prompt attention to the display of two males, each with the white clypeal bands and palpal spots scraped off, showing black integument beneath. Though all the females allowed a male to reach the part of Stage II in which he was entirely out of range of her AME, on top of her, mating was not completed in any case. However, these females on the test days rejected even normal males, and two of them proved to be already fertilized.

*Phiale flammea*. Four females paid prompt attention to two displaying males, each with



TEXT-FIG. 9. Antero-dorsal view of a female abdomen (*Phiale flammea*). The pale band acts as a director for turning the abdomen in the final part of Stage II courtship display.

the white clypeal bands and palpal spots scraped off (as in *Menemerus*); in two cases the males, during prolonged (20 minute) sessions, were allowed to reach Stage II; there were no acceptances; the females appeared very sluggish, but normal, control males were not then available for determining the females' true tone.

*Corythalia chalcea.* A female accepted promptly a male painted to resemble *C. fulgipedia,* having white pigment on the femur and patella of the normally black palps. These two species display to one other freely, but never, in numerous observations, did display proceed beyond early Stage II.

*C. fulgipedia.* A female accepted promptly a male with the white-spotted palps blackened to resemble those of *C. chalcea* (see above). Another female accepted a male with the frontal aspect, including the legs, completely covered with white. It will be recalled that in *fulgipedia* the iridescence and fringes of the legs are displayed in courtship as well as in threat. Complete blackening of the legs did not affect the female's reaction in the least, nor did removal of the fringes. In three other pairs the male was variously painted with red, from a median red spot above the AME through covering of the clypeus and palps to a complete coating of the frontal aspects (excepting the eyes) including again the legs. Once more acceptance was complete in each case, and within the normal acceptance time of the species (3 to 6 minutes).

*C. xanthopa.* Two females each accepted a male with the yellow of palps and clypeus changed to white, and another in which the clypeus had been painted black and the palps removed. When the latter male reached advanced Stage II, he could not of course proceed and eventually backed off the carapace; the female, however, had showed no signs of restlessness. Another female accepted a male with the yellow areas replaced with orange.

From these examples it appears that deviations in the color and pattern of the male play a very minor part in acceptance by the female. To summarize: In three species of *Corythalia,* altered males were readily accepted by six individuals. In *Menemerus* and *Phiale,* although mating was not completed by frontally altered males, they were allowed to reach advanced Stage II; in these two genera the available females during the tests appeared to be in non-receptive condition.

*The Role of Pattern and Color in Inter-male displays.* This aspect was investigated rather fully in *C. xanthopa* and less so in *C. chalcea* and *P. flammea.* The following results were obtained:

*C. xanthopa.* Males of A-tone responded invariably with more or less prompt threat display to the following moving stimuli in which the yellow clypeal band and spotted palps appear to be involved: conscious, chloroformed or mounted-and-dried males with yellow, orange or yellow-plus-white paint covering the front yellow areas; legs painted dark brown or black (covering iridescence); two-dimensional models of appropriate size and general shape so long as a yellow or orange bar or spot appeared across the middle; dried females painted like males; unrelated species of large size with a yellow clypeal band added; preadult male *xanthopa,* or other *Corythalia* species of similar sub-*xanthopa* size, in which males were painted like adult *xanthopa* males.

On the other hand, males responded with incomplete courtship or did not respond at all to the following stimuli: conscious, chloroformed or mounted-and-dried males with the yellow of palps, clypeus and abdomen altered to any of the following colors: red, blue, blue-plus-white, red-plus-blue; six intensities of black-plus-white which included values comparable, by Weston meter, to those of the yellow, yellow-plus-white and orange which elicit threat display; to receptive young adult females of other species of *Corythalia* painted like male *xanthopa.*

To the stimuli listed below, the reaction was variable and included incomplete courtship, threat, no reaction and a confused mixture of threat and courtship. The variability was not only between individuals, but in the same individual on different days or even at different parts of the same test period. These borderline stimuli are the following: males, or the testee's mirror image, with the yellow parts painted black as in females, white, red-plus-white or green; males with the black legs altered to white, yellow or red; females, middle-aged or old, painted to resemble males; a normal male *Phiale flammea,* characterized frontally by strong white markings on a black ground. When a male *xanthopa* face was blackened and the legs painted yellow, there was no reaction. When, as occasionally happened, a blackened, chloroformed male suddenly became conscious and threatened a normal subject, the latter either appeared startled, leaping in the air, and retreated, or, if he were courting, stopped courting and, in several instances, changed the courtship to threat display.

Male *xanthopa* in B-state responded to very few unnatural stimuli, and the few reactions which did result were so erratic and variable that no general listings would be profitable. The only invariable reaction was that orange or buff-faced males were threatened as promptly as yellow-faced examples.

The solid abdominal yellow of *xanthopa,* as seen from the rear, drew as prompt threat display as a front view; males with the abdomen striped black and yellow like females, also drew threat display. Males with the abdomens blackened, however, drew confused responses.

Unfortunately, during the inter-male series of *xanthopa* tests, which took place early in the salticid experimental period, the full

importance of the amount of mount-jerking in some species was not fully realized (*infra*). Nevertheless, in all the *xanthopa* tests, the responses did not appear in general to be dependent on the type of motion. It can be stated without reservation that the stimuli which drew the most variable, confused or inappropriate reactions (i.e., anything except threat) were almost always ineffective unless strongly reinforced by constant jerking and repeated presentations: in other words, the single twitch which in *C. chalcea* and *Phiale* sometimes made the difference between threat and courtship responses (see below) was inadequate for the less successful stimuli of the *xanthopa* series.

*C. chalcea* and *C. fulgipedia*. These two species, in one of which the palps are black and in the other spotted with white, display to each other freely, each maintaining rigidly its own threat pattern.

Under experimental conditions, the following tests were made: Two *chalcea* males each displayed promptly with threat to another male with his normally black face painted yellow (as in the smaller *xanthopa*, to which species it will not display). They also displayed to a larger male *Eustiromastix* sp., dried and mounted, his normal dark brown having a painted yellow clypeus. Again, a chloroformed, mounted male *chalcea* with the legs whitened, drew various responses from a single A-tone male; these ranged from incomplete courtship with a poorly oriented side approach, to prompt threat, depending on the motion of the mount: when the latter was not moved, attention only resulted; a single twitch was followed by courtship; continued jerking drew threat. When the same mount was presented to the same male on one of his B-tone days, the incomplete courtship responses occurred, with the previously successful single twitch, but no threat could be drawn with any type of motion. A male *chalcea's* legs were blackened, to eliminate iridescence, and the now completely black indivdual mounted on a black background, and jerked slightly before an A-tone individual. Incomplete courtship was eventually drawn, with no trace of threat.

From the above it appears that at least in *chalcea*, change of the normal black color on the mid-frontal region to white or yellow does not affect threat response, while confusion may result when the legs are painted white; this complex would seem however to be more concerned with shape than with pattern and color in the sense used in this section; the importance of type of motion is once more emphasized; the response to the mount on black seems to be connected with visibility.

*Phiale flammea*. The white scales were scraped from the palps and clypeus of two males, so that they now had in frontal view the wholly black appearance of females. Neither male was chloroformed thereafter and each was of A-tone. When placed together, both gave complete threat displays starting at three inches, followed by brief sparring, in six tests on two successive days. The displays were never mixed with courtship, except that on one day the larger, less aggressive male tended to start with a generalized display (high stance, first legs high). However, when another male was chloroformed, palps and clypeus blacked and the whole mounted, the following occurred: "A normal male took no notice when the mount was not moved. When the mount was given a single twitch, the testee hesitated, adopted a high, generalized stance, then, at one inch (unusually close) he changed into a typical crawling courtship; he continued to persistent attempts to mate, even including complete twisting of the mount's abdomen." (Field lab. note). On the second round, when the mount was persistently jerked, prompt threat response was drawn; courtship resulted once more when the movement was restricted to a twitch. Here again, as in *chalcea*, the significant difference was in the *amount* and type of motion; and as in the yellow of *xanthopa*, the median white frontal markings were, under appropriate conditions, badges of masculinity. (cf. also p. 194 for threat display toward females with whitened palps, and the role played by distance chemoperception, p. 183).

When the first legs of a normal male were painted white, incomplete threat was drawn from three individuals.

When the flame-red abdomen of a dried male was painted completely black, including the white terminal spots, prompt threat display was drawn from three individuals; the same results followed when the white carapace stripe and submarginal band were also removed. However, when the abdomen was whitened, there was no display from any of the three in a total of ten tests; one of them stalked and leapt upon it once, apparently treating it as prey, but dropped it promptly (perhaps because it was stiff). When it was re-blackened, all three males once more threatened promptly. Intensity, rather than hue, seems to be the important factor here.

The abdominal red of *Phiale* shows no evidence of being an aposematic hue. Small frogs and lizards of several species stalked and ate *Phiale* without hesitation or apparent distaste. Furthermore, a *Phiale*, in all three tests made, showed a decided fear-flight response when dropped near a young *Anolis;* this occurred several seconds before the lizard appeared aware of the spider.

The results of inter-male display experiments may be summarized as follows:

First. The light-colored contrasting clypeal and palp markings of male *Phiale* and *C. xanthopa* have definite releasing value for threat display, subject to superior control by airborne chemical stimuli and motion. White clypeal and palp markings in the naturally black-fronted *C. chalcea* have no such value.

Second. Reflected light appearing in the (to human eyes) yellow region of the spec-

trum has threat releasing value in *xanthopa*, irrespective of intensity, when occurring in the palp-clypeal region. Other spectral regions in general release incomplete or inappropriate responses.

Third. Reflected light in the red region, added to the black frontal view, does not affect threat display in *C. chalcea*.

Fourth. When the scarlet abdomen of *Phiale* is covered with black, threat responses are not affected.

Fifth. White paint applied to legs or abdomen of male *chalcea* or *Phiale* usually draws an incomplete response, or none.

Sixth. The obliteration of iridescence in *Corythalia* legs by black or brown paint does not affect display responses.

*General Summary of Value of Color-Pattern-Intensity in Epigamic Display.*

First. Pattern, color and intensity are of minimum importance in the stimulus configuration of courtship, at least in *Menemerus*, *Phiale* and *Corythalia*: Male or female "ornamentation" is not a primary or secondary releaser for either female acceptance or male courtship display, respectively.

Second. It is probable, however, that in both sexes, certain spots and patterns, particularly when correlated with motion (as in spotted palps) have definite directive and/or excitatory value, or at least function as visual aids. An example of an unquestionable directive stimulus is the pale sub-basal abdominal band which, at least in *Phiale* and *Corythalia* functions during advanced Stage II as a copulation guide for twisting the abdomen.

Third. Clypeal and palp markings contrasting strongly in brightness with the black integument and present only in the male have definite releasing value in intermale display at least in two species, *Phiale flammea* and *Corythalia xanthopa*. In two other *Corythalia*, however, one with minor markings and one with none, facial ornamentation is not a threat releaser.

Fourth. There is some evidence that at least *Corythalia* and *Phiale* have poor sensitivity in the red region.

Fifth. The application of white paint to extremities in *Corythalia* and *Phiale* sometimes affects display reactions, perhaps because of apparent form alteration.

Sixth. The obliteration of leg iridescence in *Corythalia* has no perceptible affect.

The significance of deviate responses will be discussed under displacement behavior (p. 202).

## VI. INNATE RELEASING AND DIRECTIVE MECHANISMS.

From data given in the preceding sections, the innate mechanisms in courtship and threat may now be viewed as integrated patterns. In all display, adequate physical conditions, including light, humidity and temperature, are prerequisites, as described earlier; they, as well as the general good health and nourishment of the spiders are essential and will not be referred to again in the following discussion. Courtship and threat displays as a whole will be taken up in turn, from the points of view of both sexes, followed by a more general discussion.

A. COURTSHIP.

1. Mechanisms of courtship display in males.

a. *Releasers in A-tone males of hopper groups.*

i. The stimulus must be within range of the AME.

ii. It must fulfil certain rough size-shape-distance requirements.

iii. One of the following factors tors must be present.

(a). Airborne chemical stimuli.

(b). Generalized motion (for Stage I); lack of motion is customary for advanced Stage II.

iv. The following often contribute to the configuration, but are not essential as releasers:

(a). Special frontal and/or abdominal patterns, often displayed with spe-special motions, such as the vibration of pale palp.

(b). Chemotaxis.

(c). Cessation of motion, including that of palps, often accompanied by crouching; this behavior has releasing value for Stage II, although it is not essential; close proximity is of first importance, with or without crouching.

b. *Directors of A-tone males of hopper groups.*

Groups iii and iv above are probably partly and primarily, respectively, directive in function. A light, sub-basal abdominal band is sometimes a specific director for copulation.

c. *Releasers and directors of A-tone males in runner groups.* These differ from the hopper group requirements in the greater importance of both airborne and contact chemical stimuli, as well as of proximity. The visual stimuli of i and ii remain essential, however, as releasers;

the visual stimuli of iv are probably of less importance as directors.

d. *Releasers and directors of males of lower tones.* Stimuli from all groups, acting in conjunction when necessary. Alternatively, a few stimuli may release and direct courtship display when strongly reinforced.

2. Mechanisms for courtship response in females.
   a. The stimulus must be within range of the AME.
   b. It must fulfil certain motion requirements.
   c. Airborne chemical stimuli are probably involved at close range in Stage I, at least in the runner groups.
   d. Tactile (and probably chemotactic) stimuli are essential in Stage II.
   e. No obvious secondary sexual character, including special structures, "decorations" and colors, is essential to successful mating in the genera studied.
3. Course of mutual display in courtship.

   In general, a system of progressive, mutual stimulation exists between the sexes, on the order of that demonstrated in sticklebacks (Tinbergen, 1948 *et ante*). However, in the salticids, especially in the more specialized forms, the situation is far less clear-cut. Omitting, for the sake of clarity, special exceptions and qualifications, the usual course of normal field or laboratory display in salticids is presented in Table VII.
4. Comments on various aspects of courtship.

Stage II is never entered upon without at least a rudimentary Stage I, even when it is only a resumption of a display briefly broken by the female's temporary retreat during Stage II, or even in the middle of copulation.

The role played from the female viewpoint by the size and shape of the male, as well as by his motion-configuration, has so far unfortunately proved impossible to test. The most pertinent data bearing on this are supplied by observations on the behavior of females watching males other than those of their own species in display; in each case the size and shape were similar to those of their own males, and they always retreated before allowing Stage II to commence; this subject will be further discussed under species barriers.

The female's own occasional reciprocal display during Stage I and early Stage II is not a vital factor in self-stimulation, at least in *Phiale* and *Corythalia*, since it is not of regular occurrence; it is practically absent in *xanthopa*, and only fairly common in the other two *Corythalia* species; much of the apparent display in *Phiale* females probably should be interpreted rather as distance chemoperception ("sniffing") motions with the front legs and palps.

B. Threat Display. The mechanism of threat display differs from that of courtship in the absence of positive releasing or directive value of any chemical stimuli and of the greater importance of special colors or "decorations." These badges combine with non-female behavior—i.e., height and width accentuation, plus increasing instead of decreasing activity—to release threat. The various signals, in order of importance, are general motion, motion configuration, a form-size element and, finally, any special male pattern-and-color badge. In nature, all normally act together as a configuration.

In runner genera, inter-male displays practically never occur; when they do, they are indistinguishable from courtship and break off before actual contact, probably because of the absence of female chemical releasers and/or directors. In intermediate genera, courtship and threat are usually identical until the spiders are practically touching. As in the runners, inter-male displays in these groups probably are the result of a male treating another male as a female. When the requisite close-range signals—visual, chemical or both—are not forthcoming, displacement behavior then occurs as special fighting or sparring. In hopper genera, cases of mistaken identity appear to occur only rarely, since threat and courtship are usually distinct throughout display.

C. Comparison and Comment on Innate Releasing Mechanisms in Courtship and Threat. Before proceeding to a discussion of the functions and evolution of display, it may be helpful briefly to compare the principal aspects of the innate releasing mechanisms of display.

The perceptual sign stimuli for releasing display are overwhelmingly visual in both courtship and threat, involving motion, form and size. Neither contact nor airborne chemical stimuli alone will release display of any form in the genera studied, no matter how great the reinforcement, nor how strong the internal drive. However, both forms of chemical stimuli play an important differential role in display, their importance varying phylogenetically: in general, the presence of an airborne and/or contact chemical signal is a positive differentiator for courtship, while a pattern-and-color signal in some species plays a corresponding positive role in threat. Absence of either one usually acts as a positive signal for the alternative

type of display, other factors being equal. Airborne chemoperception takes precedence over a color-pattern badge in test situations where both are present, since males court, not threaten, young adult females painted like males. Motion-configuration also supersedes color-and-pattern, since males change courtship to threat when a previously quiescent, female-painted male starts threat display. Motion-configuration itself is a strong differentiator of the two types of display, particularly in the earliest and late stages; in the middle portions of courtship (i.e., late Stage I), the tendency of some females to reciprocal display never confuses the male.

As in other groups of animals, deficiency of one signal can often be compensated for by increase in another in the same stimulus situation. An example may be given of an unnaturally painted spider, which stimulates no response when running freely in the field. When it is chloroformed or killed, and mounted, so that it can be persistently manipulated with appropriate jerks close to the tested spider, it will frequently arouse a response through reinforcement. The same situation occurs when an old female is placed with a male in a small, closed container; with either contact or airborne chemical stimuli reinforced, the male frequently displays, although he would not be sufficiently stimulated to do so in the field.

Also as in other groups, maximal stimulus is needed to arouse minimal response in spiders of weak internal drive, while spiders of strong internal drive give a normal response to a minimal stimulus, often responding to fraction of the usual configuration. As previously noted, summation readily occurs in this family.

Highly stimulated spiders in unnatural test situations, and spiders in states of moderate and low internal drive, frequently confuse threat and courtship reactions and behave inappropriately in other respects. These actions, which may often be classed as typical displacement behavior, give provocative clues to evolution; they will be considered later.

Wholly aside from test situations, however, the reaction of spiders in the field is to complex, closely integrated, mutually dependent configurational stimuli. Although there are no simple, lock-and-key arrangements, the more the stimulus situation departs from the normal, the less likely is it to release display.

In an over-all view, salticid display presents a complex combination of rigid and fluid aspects. It is true that display patterns are wholly fixed and instinctive. Learning plays no discernible part in this field of activity, since males reared in solitude perform either courtship or threat to perfection on their first attempt. Again, there is no evidence that imprinting ever takes place. Finally, when two males of different species display, each maintains rigidly his own dis-

TABLE VII.

Generalized Course of Display in Salticids.

| *Male.* | *Female.* |
|---|---|
| Becomes aware of ♀; starts display, Stage I. (*Minimal releaser*: several sight factors; airborne chemical stimuli also usually involved). | |
| | Retreats, or watches ♂, usually in braced, high position, often vibrating palps. Rarely attacks. (*Minimal releaser and director*: several sight factors). |
| Approaches, in zigzags, or follows (if female retreats), continuing or resuming display. (*Minimal releaser and director*: above sight factors, plus type of female motion or lack of it). Special ♀ signs, such as vibrating palps and light abdominal spots probably have directive value. | |
| | Becomes completely attentive; sometimes gives weak reciprocal display. (*Minimal releaser*: summative effect of display motions). |
| Speeds up display tempo. (*Releasers and directors*: reduced motion of female, plus chemical stimuli. Self-stimulation is doubtless also a factor). | |
| | Ceases motion and, usually, crouches low, legs drawn in. |
| Enters Stage II. (*Releasers*: primarily, proximity of female; also involved, usually, her lack of motion, low position, and, doubtless, reinforced chemical stimuli). Copulation follows unless female withdraws. (*Director*: sometimes a pale abdominal cross-bar). | |

play pattern; no temporary modifications were ever seen to occur; by contrast, imitative behavior is frequent in vertebrates, as in the cormorants which altered their flight pattern to match that of their pelican companions (Beebe, 1938, p. 106).

Nevertheless, in working with living salticids, both their own individuality and the dynamic, unfinished, untidiness of display mechanisms are constantly apparent. A given spider's behavior is scarcely more predictable than that of a single electron. It depends, at any given instant, on great numbers of factors, external and internal, all in various stages of evolution, all related, and all themselves in a state of constant change. Wasted energy, abortive displays and lost opportunities are the rule. Altogether, the lumbering, complex, display mechanisms do not appear efficient. The most that can be said of them is that they work adequately enough, often enough, to ensure the perpetuation of the species. In the end, however, all the billions of salticids, hopping at this moment about the globe, are lively proof of their success.

## VII. BEHAVIOR RELATED TO DISPLAY.

The basic similarity of behavior trends in all higher organisms—whether invertebrate or vertebrate—becomes increasingly clear. Not only do animals agree in the obvious, basic activities essential to all life, but they prove also to be surprisingly similar, among the end forms, in the more complex aspects of behavior. It has long been recognized that when vision becomes the dominant sense, elaborate, visually dominated courtships often evolve; the principle applies in certain cephalopods, crabs, spiders and insects as well as among fish, lizards and birds. The importance and frequent distinctness of threat display in salticids has been emphasized throughout this paper, and is in accord with results of recent behavior studies of birds and other vertebrates. Similarly, it is increasingly evident that dominance hierarchies, social and territorial behavior and displacement activities very often occur in higher invertebrates, though usually in primitive form. Although these latter aspects were studied only incidentally in the Rancho Grande salticids, the following observations appear to be worth recording.

A. Displacement or Substitute Behavior. Experimental work sometimes drew inappropriate responses which correspond closely with typical displacement behavior in birds and other groups. When a stimulus configuration, while partly effective, was yet too exaggerated or incomplete to draw an appropriate display, the spider either retreated, attacked or by-passed the stimulus, exchanged threat for courtship and courtship for threat or regressed to a more primitive level of display behavior. It is interesting, however, that at no time were the substitute activities wholly outside the sexual field. That is, never did the spider stalk an insect, pick up a discarded fly, spin a retreat, or even resort to grooming—that substitute action so common throughout much of the vertebrate world.

This restriction of displacement behavior appears to be an example of the rigidity typical of higher invertebrates. The compartments of life are kept distinct even in the midst of "mental" confusion, shock or frustration. With such restrictions, a girl would not reach for her lipstick when frightened by a bomb, nor a startled bird fidget with the makings of an off-season nest. To lapse into anthropomorphism, a salticid, when his prey escapes, never picks a fight with another male, nor does a rejected suitor gorge on extra flies.

B. Dominance. In salticids, little hint has yet been found of long-term dominance relationships. Day to day variation, as shown in energetic courtship and threat or apathy and retreat, is on a rhythmic, physiological basis. It is true that some males never develop as high tone levels as others, the peaks of their rhythm curves being lower; in this sense dominance may be said to occur. I have never found, however, that rank is altered by a series of successes or failures in threat display or in actual combat. In primitive groups, where inter-male combat does not ordinarily exist, nothing approaching dominance relations was seen (apart from the usual physiological fluctuations, which determined the degree of courtship activity at a given time). In groups of young and old spiders placed together in a cage, the small ones invariably showed a healthy wariness of the large individuals; in view of the carnivorous character of the spiders, however, this behavior certainly needs no more explanation than the obvious one of self-defense. (See also p. 203).

C. Sociality. *C. xanthopa* was one species in which traces of social behavior occurred. Along the leaf-strewn Water Trail, the richest habitat for this species, three to ten individuals were often found fairly close together. These groups included individuals of various ages and both sexes. They occurred in an area of about a square yard or two, divided by 10 to 20 feet from the next group. There was absolutely no discernible difference in the ecological characteristics of the populous and barren stretches, and indeed they shifted back and forth in quite irregular fashion over a period of weeks. Intra-specific relations within a group appeared purely casual. Abortive courtships and threat displays were brief and frequent. There was a high degree of mutual toleration, but, except for sexual situations, no inter-individual associations. It is noteworthy that quite small individuals, measuring less than half the size of the adults, were included in these groups, and apparently not stalked as food. Often their attention was attracted by the

displays of nearby adults, and at times they appeared to watch attentively these encounters of their elders, although they took no part whatever. The same behavior was noted in non-displaying adult males, and in fat females, obviously soon to lay eggs. On other occasions, these non-displaying members of the group simply continued their previous occupations, paying no attention to the others; they either maintained hour-long lookouts from the top of a projecting twig, stalked prey with indifferent success, hopped slowly along a meandering course, or simply moved occasionally out of the shifting sunlight.

An example of more advanced sociality was found in *Semorina megachelyne*. A large silk shelter was taken containing a group of 14 individuals of various instars, including several adult males and females. The young ranged from the first through the preadult stadia, the youngest being sheltered in a subcocoon. The morphologically primitive position of *Semorina*, compared with the advanced niche of *Corythalia*, indicates that sociality is not dependent in this group on phylogenetic specialization. Comparable dissociation of these two factors is found in other groups, including non-salticid spiders, lepidopteran caterpillars and birds.

It is probably significant that in neither of these examples of incipient sociality, *Semorina* and *Corythalia*, is inter-male fighting developed; in the one case the males follow the primitive pattern of mutual disregard; in the other, combat has been sublimated into threat. Never have I seen any signs of group formation in the more pugnacious genera.

D. Territory. A territorial concept almost certainly exists in salticids, but work has scarcely been started on this angle. In captivity, all salticids generally returned to the same shelter, if they made one, night after night, even occupying it through several successive molts, so long as it was undisturbed. It seems probable that such a practice occurs also in the field. It is certainly a likely beginning for a concept of territory, or at least of home range. When siblings of *Phiale, Corythalia* and *Eustiromastix* young were reared in groups of three or four through the early molts, they not only got on peacefully at all times, but each always—on the many occasions when they were observed with this point in mind—returned to his own shelter at night and during ecdysis. One group of three *Phiale dybowskii* was reared to adulthood in this fashion. Individual variations in size and pattern made the identification of individuals easy after the second instar.

Cannibalism is exceedingly rare in this family, and when it occurs it is only under extreme provocation of hunger or gross size disparity. In the few cases where females killed the males, they were eaten only twice, both in *Eustiromastix*. After inter-male battles, the losers were never eaten, even when they had been disabled or killed.

On the other hand, there is no evidence yet that salticids actually defend a territory, even in the case of adult males. I am quite sure that the young at least do not have one, although the concept of home range seems applicable, at least in *C. xanthopa*. This term, as defined by Burt (1943), signifies that wandering of individuals is limited, although the area is shared at least tolerantly with others of the same species.

It is notable that although in the orb-weavers the adult males wander, in *Corythalia xanthopa*—the only species where field marking has been initiated—the females did the roaming. One female, recaptured after 34 days, was taken 186 feet from her original location, while several marked males were seen repeatedly during a single month within two feet of their original positions. A similar situation exists in fiddler crabs (Crane, 1941, p. 160) and, of course in vertebrates (e.g., Evans, 1938; Lack, 1943).

When a strong adult male *xanthopa* in A-tone was dropped close to a wild male who had hitherto been undisturbed, the usual threat display took place, but I saw no sign whatever that the strange male was usually driven off by the previous "tenant," or showed much perturbation. The response was tested more than ten times. This result is in strong contrast to the behavior of an orb-weaver dropped into a strange web. The retreat of a protagonist seemed to depend only on his physiological condition, rather than on any general reduced pugnacity or sense of security when out of his own range.

The other intermediate and hopper group salticids were in general strongly individualistic; two or more adult males were rarely shaken from the same herb or bush, and it may be that in these cases definite territories are maintained and defended. On the other hand, possession or invasion of a territory is certainly not a prerequisite to display, judging by the prompt reactions of A-tone males dropped simultaneously on a strange table-top. Altogether, development of territoriality appears to be a very primitive level.

## VIII. FUNCTIONS OF DISPLAY.

### A. Courtship.

The theories concerning the functions of courtship display in spiders have already been reviewed (p. 170). The conclusions resulting from the Rancho Grande studies are as follows: First, courtship display is unquestionably a necessary preliminary to mating, and not merely an outlet of excess energy for males in breeding condition, as suggested by Wallace and Berland. Second, sexual selection in the original sense used by Darwin and the Peckhams is not operative. Third, as Savory points out, the concept of recognition as distinct from, and preceding stimulation, does not appear to be necessary.

Indeed, any concept of preliminary recognition seems to be highly questionable, even when recognition is regarded merely as a kind of realization by the female that a potential meal is not at hand. Rather, it seems probable that it is through her sexual stimulation that her feeding impulses are inhibited. In this view, the two processes are merely different results of the same psycho-physical sequence, developing simultaneously and governed by the same stimulus configuration. To distinguish between recognition and stimulation in salticids seems as difficult as to differentiate temporally between human fear and loss of appetite when a charging bull interrupts a picnic: in each case two emotions, or at least sensations, are involved, one positive, one negative, and bearing an inverse ratio to each other.

As modern observers agree (e.g., Savory, 1928), the stimulation of the female is probably physically as well as psychologically necessary, since alterations appear to be made in the epigynum itself in order to permit the insertion of the palps.

The following summary may now be given of the functions of salticid courtship, as they appear from the Rancho Grande studies. It is, in essence, a selection and elaboration of certain earlier views, especially those of Savory and Bristowe. Most of it applies to animal courtship in general. The term "courtship," as used throughout this paper, includes the responses of the female as well as those of the male, and the production as well as the reception of sign stimuli.

The primary functions of courtship in salticids, then, may be expressed as follows: Courtship serves to bring to mutual attention and proximity two individuals of the same species, opposite sex and requisite physiological condition; simultaneously it inhibits their usual predator and self-protective behavior while stimulating each sex so that copulation may take place. These are the primary functions, of obvious and immediate biological use in the life of the individual.

Secondary functions, which may be considered by-products of the above, are of importance in the life of the species. First, sexual selection operates in the sense that males of chronically mediocre drive—among which are doubtless individuals of genetic weakness—do not use sufficient energy and persistence to win acceptance by females. Second, courtship display acts as an effective isolating mechanism between similar but well-evolved species: Since crosses would, judging by analogy in other animals, often prove sterile or unfit, the progressively exclusive action of individual courtships must prevent considerable germ cell wastage. The effectiveness of display as an isolating mechanism will be discussed in the section on evolutionary aspects.

### B. Threat.

Earlier views on the cause and function of fighting and/or threat display among salticid males were summarized on p. 170. To recapitulate briefly the two extreme hypotheses, the Peckhams accepted the unmodified Darwinian premise that inter-male fighting was brought on by rivalry; as a result, the females mated with the strongest or bravest or boldest, either through male conquest or female choice. Bristowe, on the other hand, holds that inter-male display occurs when males temporarily mistake each other for females; actual fighting sometimes results through frustration.

Neither of these views explains satisfactorily the condition in many salticids, including *Corythalia*. Against the Darwinian hypothesis stand the facts that the winner of a combat does not necessarily get the adjacent female, females certainly do not necessarily "choose" the winners, the fights are usually no more than slight psychological sparring matches, at which females may or may not be present, and the winners—that is, the more aggressive—are certainly not necessarily the largest or brightest of the males. I have seen a six or seven-legged male, of small size, prevail over larger individuals on successive days; almost certainly the epigamic physiological rhythm was involved; but some individuals appear regularly to be more dominant (in their A-tone periods) than others of the same threshold. (See also p. 202). In the species Bristowe observed in England, courtship and threat display were identical. For such as these, his hypotheses of mistaken identity is completely satisfactory. According to the hypothesis of phylogeny presented in the present paper, these represent an intermediate phase of development of dependence on sight practically superseding dependence on chemical stimuli. In genera taken to represent more primitive forms, such as *Menemerus*, *Ashtabula* and *Semorina*, all far more dependent on chemical stimuli, threat display is apparently nonexistent and mirror display never occurs (except in self-stimulation in *Menemerus*, p. 182). Finally, in the most visually dependent genera, the hopper groups, of which the best ultimate examples are in *Corythalia*, threat and courtship are completely divorced. In *C. xanthopa* such an extreme is reached that different appendages are used in the two kinds of display, and true fighting has never been known to occur except under extremes of crowded, hot laboratory conditions. It seems that here there is a sublimation of aggressive impulses, as in many birds, and that a type of mutual stimulation takes place which is useful in maintaining or increasing sexual tone.

Just as in courtship display, it must be kept always in mind that male spiders are potentially dangerous to one another, both because of their carnivorous habits and their poison glands; this is rarely the case in other

groups of animals. Where mistaken identity in salticids results in actual fighting, with consequent frequent casualties, the following conclusions concerning its functions appear to be valid. All of them are of the secondary type, of importance to the species, rather than to the individual.

1. The elimination through disability or death of weaker males, thus strengthening the strain through natural selection.

2. The prevention of weaker males mating as often as do stronger individuals.

3. The encouragement of excess males to go elsewhere in search of mateless females, and so ensuring the more even distribution of the sexes.

These three points conform to Darwin's general hypothesis, excepting only that females do not deliberately choose superior males. Although it is true, as Bristowe and others maintain, that actual fighting, to the point of inflicting injury or death, is rare among spiders, it most certainly does occur, under natural conditions at that, among some salticids at Rancho Grande. For example, an apparently new genus near *Capidava* (not yet described) time and again fought to the death in large display boxes and on open table tops; twice they were seen fighting beside trails in the forest; in one of the latter cases a male was killed; in the other both were injured.

In the majority of salticids, and especially in *Corythalia*, where threat display is highly ritualized and actual fighting occurs only rarely and atypically, the physical elimination of males does not take place. In these cases, the threat display undoubtedly represents an advance over the more wasteful practice of actual fighting.

In these ritualized displays, the additional function of maintaining emotional tension is probably of importance to the species as a whole, although it is not necessary to individuals. Perhaps males having frequent opportunity for epigamic display maintain A-tone for longer periods. Armstrong, 1947, discusses tone maintenance in birds and gives excellent examples. No experiments whatever appear to have been done on this question in spiders, but its importance is becoming increasingly recognized in other groups. Experiments at Rancho Grande proved only that threat display is not a prerequisite to successful mating, either from the male or female point of view. *Phiale* and two species of *Corythalia* all showed conclusively that virgin males displayed promptly and completely to virgin females and were accepted by them, without any of the males ever having seen another male, much less practised or observed threat display. Each of the individuals tested was reared through at least three previous instars, and permitted to molt to the adult, in complete solitude. Precautions were taken, as in all display experiments, to eliminate the danger of chemical stimuli remaining from previous spiders.

Conversely, virgin male *Phiale*, *C. chalcea* and *C. xanthopa* performed threat display perfectly to virgin males of their own species without ever having laid eyes on or received chemical stimuli from a female or another male.

Nothing is known of territoriality in any of the species except in *xanthopa*: here it appers to exist, but in rudimentary form (p. 203). This amount, however, might account for the development and maintenance in this species of a completely separate threat display. But it seems certain, as said above, that at least equally important to the species is its function of mutual stimulus and of keeping males to some pitch of excitement, perhaps in a state of long-sustained A-tone for dealing with wandering and scattered females. There is no question but that males tend to display to each other more promptly in the presence of a female: in photographing threat displays, one female was always placed with the two male subjects, since females were repeatedly found to have this decided catalytic effect. Often the males spent more time displaying to each other than to the female.

Another function of threat display doubtless is its usefulness as a "safety valve," its displacement behavior aspect, for spiders already keyed to display pitch (p. 202).

No true group displays, comparable to those reported by the Peckhams (1889, p. 40) for several dendryphantinids, were seen at Rancho Grande. They undoubtedly should be regarded as rudimentary social affairs, again with the double function of inhibiting hunger and stimulating sex.

## IX. EVOLUTIONARY ASPECTS OF DISPLAY.

The purpose of this section is to interpret salticid display from an evolutionary point of view. Although the dangers of top-heavy generalizations are fully realized, it seems advisable to organize the limited data availbale. As Menninger puts it, "Classifications must never be taken too seriously—but the fear to use them has prevented much more thinking." (1945, p. 34).

### A. Hypothetical Philogeny.

While many display similarities obviously coincide with natural affinities, others reflect only an extensive parallelism among the subfamilies. The salticids show a "bush type" of evolution, with similar basic trends in each branch.

The parallelism is well shown in the locomotive, sensory and display differences that have been discussed from time to time in this and preceding papers (Parts II and III). At Rancho Grande, *Menemerus*, *Semorina* and *Ashtabula* are examples of the apparently primitive "runner" group; *Sassacus* and *Phiale* are intermediate forms; and *Corythalia* and *Mago* are advanced "hoppers." Each of these groups contains representatives of two or more subfamilies, and each

subfamily usually includes genera in two or more groups. Their various characteristics will now be assembled.

The "runners" never jump or hop during horizontal progress except to cross a gap or leap on prey. According to experiments, they depend more on chemotaxis than do the other groups, court less readily in its absence, rarely or never respond to a mirror image and are rather strongly affected by the loss of their palps and first legs. The first legs are often held in front of them, not helping in locomotion, but barely clearing the ground, while the palps may pat the ground lightly. When in a strange place, they run to and fro, palpating ceaselessly and appearing endlessly "restless" and "nervous." Although they stalk and leap on prey like the hoppers, they nevertheless tackle large prey in preference to small. *Menemerus* chooses moths and the larger Diptera instead of *Drosophila;* in captivity, when no choice is given, they miss fruit flies repeatedly and eventually become thin. Large, hopper-group *Corythalia* of similar size, in contrast, can live out their lives on a fruit fly diet, catching them with ease. Morphologically, the most obvious characteristics of the runners are low carapaces and few, weak leg spines.

The intermediate group seems to be in the middle of changing from moderate chemotactic to nearly complete visual dependence by way of distance chemoperception. They are long-sighted, hop when hard-pressed, pursue their mates via efficient short-cuts and are relatively little affected in display when deprived of palps and first legs. Yet they appear to gain chemical sense impressions from a distance largely through these members which, from the second instar, often wave in the air during normal exploration. *Phiale*, when near mates or food, before display or stalking begins, is especially prone to wave the first legs up and down. It seems probable that they are "sniffing" the air. Berland's accounts of *Philaeus chrysops* and others (1914, 1923, 1927), waving their legs when completely alone in clean boxes, sound as though these were intermediate-group spiders. *Philaeus*, incidentally, is a close relative of *Phiale*. Bonnet's (1933) *Philaeus*, studied in another part of France, never waved the legs except in true display; why these observations should differ so radically remains, for the present, a mystery. Berland's *Saitis barbipes* waved the *third* legs at random, as well as in display.

Among salticids generally, it may be that the female is "sniffing" the male when during display she often vibrates the palps and first legs; if so, the sense of distance chemoperception may evolve through the female. Certainly in the runners, the female's palps are usually particularly active, whether or not they quite touch the ground in true chemotaxis. It does not seem advisable to consider this activity solely as a symptom of nervous tension.

The "hoppers" are the visually dominated salticids; chemotaxis means little or nothing to them under natural conditions; distance chemoperception operates as a secondary releaser for courtship display. Their sight is magnificently developed, and their courtship sign stimuli overwhelmingly visual. These are the "poised" spiders; they sit quietly when dropped on the table, look about them, then hop away, at leisure and with frequent pauses, interspersed with a measured walk. All eight legs remain firmly on the ground except during a hop or display; there is otherwise no raising at all of the first legs, or carrying of them clear of the ground. Carapaces are high and leg spines strong and numerous.

An inspection of Table II and Text-figs. 2 and 6 will show that among runners courtship is simple and threat practically nonexistent. In intermediate groups, actual fighting is frequent, but its early stages are little or not at all differentiated from courtship. In the hoppers, true fighting is rare and special threat display the rule.

The divisions appear to be based primarly on the different degrees of visual dominance. The eyes in each successive group seem to take over more and more from the chemical senses. And it is the dependence on the latter which appears, both functionally and morphologically, the closer to the pre-salticid stock. But, as in various studies of animal and human societies, the forms in midevolution seem most subject to combativeness. They appear to be in the middle of changing from one way of life to another, mistakes are made, frustration results and combat ensues.

One vitally interesting clue to the evolution of salticid display is given in the behavior of the highly specialized hopper, *Corythalia xanthopa*. Senile, over-stimulated or low-tone spiders often use primitive chemotaxis during courtship to the frequent and inappropriate exclusion of other sign stimuli (p. 178). These and other hoppers in a similar condition tend to leap at threat stimuli rather than perform their characteristic displays. This behavior seems unquestionably atavistic, regressive in a phylogenetic sense. Similar examples among displacement behavior (p. 202) consist in the replacement of threat with physical attack in experimental situations.

### B. Origins of Display Motions.

The biological principle of least effort, as presented by Zipf (1949), proves to be of considerable help in this attempt to understand the development of salticid display. The subprinciples of permutation (i.e., combination) and multiple function seem especially applicable. Armstrong in particular has implied their operation throughout his discussion of bird display (1947, e.g. p. 61).

From this point of view, display evolved through the use, with modification, of actions, senses and structures already serving

less specialized purposes in the economy of the organism. Only rarely would a display action evolve especially to fill an epigamic need.

In direct agreement with this general concept is Bristowe's view of the origin of salticid display. It appears to him that the rituals grew from the groping and fending-off motions of the primitive stock. Certainly, it seems far more likely that display grew from gestures like these, which had a different original function, than that an entire new series of motions arose for display alone.

The acceleration and exaggeration of simple motions, so typical of display, are clearly related to the excitement, to the nervous agitation, connected with breeding activity. The difference between this view and those of Wallace and Berland is that, to them, display appeared to have no function; it was simply an expression of high vitality or excitement.

The "groping" motions certainly included chemotaxic behavior, such as is used by many runners in casual exploration as well as in responding to the trails of females. The similar behavior of very young runners, just out of the cocoon, contributes largely to this conclusion. Again, high-in-air leg waving, found in numerous displays throughout the family, seems to have an undoubted origin in distance chemoperception of airborne stimuli.

Plausible origins of a number of other common display gestures may be proposed. Thus, the vibration of palps originated in the "sniffing" motions so characteristic of chemoperception, including both contact and distance types. The vibration is perhaps also useful in dissipating nervous tension during courting excitement.

Twitching or lowering the abdomen is another frequent display gesture which may be due to permutation. Probably it was concerned originally only in attaching silk to the substratum, in the usual salticid fashion of ensuring a quick escape. An almost universal part of display is the habit of approaching a female in zigzags, which obviously gives added time for necessary stimulation. When zigzagging was first combined with lowered spinnerets, it is easy to see how a side-swinging abdomen could have developed: in the more primitive, long-abdomened Dendryphantinae, it seems a natural result analogous to that of a train rounding a bend.

The elevation of the abdomen is characteristic of all the ant-mimicking or pseudoscorpion-like salticids in which display is known. It was also typical of normal progress in *Semorina* and related genera as early as the second instar. Its ultimate origin is not yet clear. Possibly the gesture started as the end of the dropping motion, as a spider hits the ground at the end of a silk cable. Possibly, actual scorpion or pseudo-scorpion mimicry was involved among larger forbears; these hypothetical spiders may well have been large enough to win a mimic's protection from frogs and lizards (cf. Part III, p. 37).

Again, it is possible that abdominal lifting, quiverings, and even the swift rockings of some displays are concerned in the emission and wafting of a chemical display signal. I have as yet no corroborative experimental data; work with sealed genital grooves and epigyna—a promising approach—has not been adequate. The possibility is mentioned here as a potential X-factor, an "etc." that may prove important.

In *Lyssomanes* the retinal motion within the light-green, antero-median eyes seems to play a definite role in courtship. The resultant color shifts increase in tempo with excitement. They seem clearly to be a ritualization of incidental effects resulting from the mechanics of vision. Although the same motions occur throughout this and other large-eyed families, they are rarely as noticeable because of the dark pigment which usually surrounds the retina. The morphological basis has been discussed by Homann (1928, p. 235).

All of the display motions mentioned up to this point can have evolved through permutation of activities normally occurring in the simplest epigamic situations as well as in other fields—dropping from overhead, fixing a silk drag-line for quick escape, groping forward, and so on. In this way these postulated display origins parallel the epigamic character of displacement reactions (p. 202). Several possible exceptions will now be discussed.

The display crawling motion may have originated from the hunting rather than the sexual field of behavior. In this phase, the male lowers the carapace and creeps directly forward. Usually it occurs during late Stage I or early Stage II of courtship. It crops up sporadically, with variations, in almost every subfamily observed. It may have grown from a displaced stalking motion, definitely outside the sexual field. It appears more probable, however, that there is a sort of innate, anticipatory imitation: the crouch is extremely similar to that usually assumed by the female during the latter stages of courtship. As in many birds, this position often acts as an important releaser for the latter part of the male's display. Its previous assumption by salticid males, in combination with a typically masculine approach and leg stretching, perhaps has value in empathically inducing the female to assume a similar position. Whatever the origin, this motion is one of the most remarkable in all salticid display.

Two widespread groups of display gestures do not seem to be based on economical permutation, on made-over motions. They are the lateral leg displays and the stretchings up to maximum height. It seems, rather, that these salticids have evolved independently the widely successful animal custom of ap-

pearing larger than life in a crisis. It is exceedingly interesting that they never use the technique in other departments of living; never do they display before prey or hungry enemies; in salticids, the "big bluff" is reserved solely for an epigamic crisis.

Posing is a frequent occurrence in displays of the size-increasing type, particularly in threat and especially among the plexippinids. The motionless state, amounting to a kind of catatonia, often persists for many seconds after the exciting object has been removed. Similar behavior occurs in many animals under various conditions; it has been discussed at length by Armstrong in connection with bird display (1947). Its origin in salticids remains obscure.

This effect of seeming larger—whether in connection with courtship or threat—is of special interest in comparing displays within the advanced genus *Corythalia*. Courtship and threat display are distinct in the three species studied. However, in *xanthopa*, courtship is simple and primitive, exhibiting only the first two legs, while the remaining pairs, all specialized, are reserved for the highly developed threat display. In *chalcea* and *fulgipedia*, on the other hand, the first legs are used only in Stage II of courtship, while more posterior legs take part in Stage I of both courtship and threat. It seems that *xanthopa* represents the more primitive form, with the size-increasing threat fan occurring first. Then, by permutation with modification, the original threat function was extended, in the other species, to form a more complicated courtship. In support of this hypothesis, *xanthopa* appears decidedly more generalized than the other two species in several structural and developmental characters; these include eye proportions, spinulation, course of color development and dentition of tarsal claws.

The displays of two advanced Dendryphantinae give similarly interesting clues to their relative evolutionary status. One species, *Sassacus ocellatus*, shows a vestige of the side-swing typical of the subfamily; in the other, *S. flavicinctus*, no swinging occurs. It is the latter form which is morphologically more advanced.

The subject of vestigial behavior characters is, of course, one of the most controversial. Which traits are to be considered vestigial and which rudimentary? One point, however, appears increasingly clear. Any successful animal species includes in its organization a hodgepodge of behavioral relics in addition to the usual morphological trash. When a dog revolves before lying down on a grassless rug, he is performing a well-worn example of a functional antique. Similarly, *Sassacus*, in a moment of face-to-face courting, swings his stubby abdomen sideways, even though it and its ocellus are well hidden behind the sturdy legs; surely this example belongs equally in a behavioristic museum.

### C. Relation of Secondary Sexual Characters to Display.

The question of vestigial characters leads directly to the problems of ornamentation, where morphological and behavioral relations are even more involved. Some "ornaments," including the fringes and iridescence on the displayed legs of *Corythalia*, are probably recently evolved structures: they are highly variable in individuals; their adaptive value is so slight that it has not been proved experimentally to exist at all; they develop (as do most epigamic characters) only in the final instar; and they are confined altogether to males. Yet their place in the perceptual sign situation seems unquestionable; on a mathematical basis these recent refinements would doubtless prove to have definite adaptive value, at least to the extent of making their possessor more conspicuous during display.

Next to these come such signs as the yellow or white clypeal bands of *C. xanthopa* and *Phiale* males, which have decided, contemporary releasing value for threat display.

Finally, in a confusing mixture, comes the mass of "decorations," including vestiges, characters linked genetically to selected structures, patterns aiding in camouflage, and mere byproducts of metabolism. Only rarely can their origins be satisfactorily discovered or inferred. They include the sex-chromosome-controlled tufts of dark-phase male *Maevia vittata* (Painter, 1913), the scarlet-red of *Phiale* abdomens and the circles of colored scales around most salticid eyes. These circles occur as early as the second instar and are irrespective of sex. Possibly, among primitive salticids, they had adaptive value, making the large eyes or frontal regions more conspicuous in display; now they have no demonstrable function, and their early appearance, far back in ontogeny, indicates a vestigial, if not a purely metabolic, character.

A related instance is the occurrence of white scales on the legs of intermediate instars in *Corythalia*, followed by their obsolescence on the front of legs in adult males; they may well represent an old secondary or minor display character which has been superseded by iridescence; a similar explanation may apply to the reduction of clypeus white in adult male *chalcea* and *fulgipedia*.

The variable distal abdominal ocelli of *Sassacus ocellatus*, mentioned above, seem to belong rather definitely among the vestigial character group.

All of these relics, again in agreement with the principle of least effort, persist unless it takes less "effort" for the organisms to drop them than to carry them along

The old question as to the significance of elongate chelicerae recurs. Bristowe has pointed out that they are only rarely used in courtship or fighting, and also are unquestionably less efficient than those of the usual size (1929, p. 339). It seems to me that

they are enlarged, not to aid fighting, but much as first legs are specialized, primarily for an increase in conspicuous area. It appears, too, that secondarily their very inefficiency may be adaptive in the way that a threat display is adaptive: the danger of mutual injury is reduced without reduction of the presumable toning value of aggressive behavior.

It is noteworthy that these enlarged chelicerae, in the genera with which I am familiar, occur in the middle groups: in the Dendryphantinae, and in *Salticus* (morphologically an advanced marpissinid), in which aggression reaching the contact stages is most developed. Elongate jaws occur also in the highly aberrant lyssomaninids, but I have never been able to induce any threat display in them whatsoever. Another point is that in some genera, for example *Sassacus* and *Ashtabula*, the length of the chelicerae is highly variable among individuals, exactly as in certain beetles (e.g., Beebe, 1947) without any reference to their general tone or health. No use as a specialized, female-holding tool, as is found in *Pachygnatha*, has ever been observed in a salticid.

In salticids, as seems increasingly clear in other groups, function appears basic, structure follows after. The male salticid raises his forelegs or middle legs, or jiggles his palps; elongation, thickening, blackening, whitening, polishing or fringing may or may not follow. A spider does not, as the older naturalists naively implied, show off his decorations; rather, his decorations evolved in a conspicuous position. Every experiment made in this study showed that motion—function—was of more importance than morphological detail. This view does not, of course, rule out the obviously great reciprocal influence of behavior and morphology during selection. Nevertheless, in any general trend, it must be the function which usually changes first, while vestigial tufts and spots, seemingly placed to accent an obsolete display, persist indefinitely.

### D. Sexual Dimorphism and Display.

The correspondence in forms of sexual dimorphism in both salticids and birds was discussed at length by the Peckhams (1889, 1890). Here their general points will only be summarized and remarks made concerning the relationship of dimorphism to female behavior. As in birds, dimorphism is of three principal types. First, and apparently most primitive, neither sex is strikingly marked, or greatly differentiated in secondary characteristics; display is primitive and the female remains completely passive (examples: *Semorina, Mago*); in the second type, sexual dimorphism is strong, the female remaining dull and adolescent in coloring and her behavior passive (examples: *Sassacus flavicinctus, Plexippus paykullii, Corythalia chalcea*); in the third, both sexes are strikingly marked and similar, with the female often acting aggressively or, in advanced groups, tending to reciprocal display with the male (examples: *Sassacus ocellatus, Corythalia fulgipedia*). However, there is by no means a fixed correspondence between female aggression and striking pattern: for example, the most aggressive females found at Rancho Grande were those of *Eustiromastix* sp.; structurally, this species is strongly dimorphic with the females dull and little differentiated from the young; they always killed the males shortly after mating if kept together, and, in courting, the males had to be excessively cautious. A similar situation occurs in some dendryphantinids (cf. Peckham, 1889). As in birds, all degrees of dimorphism, both of morphology and behavior, can sometimes be found at low taxonomic levels, including the genus. It seems certain that hormones and neurohumors are as deeply concerned in these characteristics as in vertebrates.

### E. Climate and Display.

Another interesting aspect of phylogeny refers to a possible effect of climate on the development of display. It seems likely that there are fundamental differences in behavior in the tropics and in the north, which may well be responsible for some of the differences between the Rancho Grande observations and those in the temperate zone.

The differences in breeding season length is usually considerable. At Rancho Grande it is months long, while in the north the adult males are often active only a few days or several weeks. In the short-summered north the relatively few salticids which adapted themselves to the severe winters also had to adjust in less obvious ways. Basically this meant the more perfect coordination of the breeding mechanisms of the two sexes; in a short season there would be little time for the vagaries of physiological rhythms or of regressive behavior, both of which are so evident at Rancho Grande. Also, in a climate where many individuals of few species are the rule, instead of vice versa, there would be no economy in restricting a female to the single insemination which appears typical at Rancho Grande. Again, the same northern conditions might encourage the development of the almost communal displays described by Peckham (1889, p. 40), and which I have never had the fortune to see in the tropics. It must be remarked, however, that communal displays in birds reach a high tropical development, as in birds of paradise and cocks-of-the-rock.

Finally, in the brief northern summer persistent courtships and protracted fights apparently are usual, from accounts in the literature. By contrast, in Venezuela courtship and threat displays are almost always short; either they are unsuccessful, which is usually the case, and quickly broken off, or else they are consummated in a few minutes. This difference is probably also tied up

with the leisure of physiological rhythm in the tropics, with the lack of a pressing hurry to coordinate the mechanisms.

### F. Displays as Specific Barriers.

Almost every student of salticid behavior is familiar with the frequent occurrence of display between different species, both in courtship and in threat. At Rancho Grande, it was found that in general any A-tone male would initiate appropriate display before any moving male or female that showed a few sign stimuli roughly similar to those of its own species. The females, presumably because of the chemical factors, were invariably close relatives; the males, in inter-male display, had to conform in appearance only. The heterosexual pairs of species which displayed regularly to each other, under unconfined laboratory conditions, were the following: *Corythalia chalcea* and *C. fulgipedia; Plexippus paykulli,* female, and *Eustiromastix* sp., male; any two species of *Phiale.*

This weak selectivity would, on first sight, seem to indicate that differences in display have little value in erecting or maintaining specific barriers. Closer study, however, results in the following observations.

First, display is only initiated; it is rarely carried on beyond early Stage I. When it is continued longer (in courtship only), by a male of exceedingly high tone, the female always breaks away well before the end of Stage II. Even in experimental situations with chloroformed females, the male himself was never, in more than a dozen trials, seen actually to copulate; it seemed that in each case a mechanical barrier was reached in the epigynum. On the other hand, fertile eggs were secured after copulation with chloroformed females in one pair of *Eustiromastix* sp. and one of *Corythalia chalcea,* showing that the drugged condition of the female was not the final deterrent.

Second, when individuals of their own species are introduced to a pair of mismatched displaying spiders, attention is quite promptly turned to the appropriate newcomer.

The above does not of course show that inter-specific crosses may not occur in nature; it only indicates that, if they do so, they are probably unusual in the area studied, even though several pairs of closely related species occur, each having similar displays and occupying overlapping ecological niches. These include *Phiale dybowskii* with *Phiale* sp.; the latter with *P. flammea;* and *Corythalia fulgipedia* with *C. chalcea.*

The particulate nature of display explains its apparent inefficiency. It does not act as a single unit, but rather as a series of strainers of progressively finer mesh. An interspecific display is interrupted when the constantly changing stimulus configuration—releasing, directive or both—becomes too weak, from the viewpoint of one partner, to draw the requisite response. This positive response may, of course, appear active or passive, depending both on the stage of display and on the sex of the partner. The point at which the display breaks off depends largely on the physiological conditions of the two protagonists.

It was pointed out on p. 204 that display may aid in the economy of germ cells by preventing unproductive mésalliances. It seems clear, however, that as a practical barrier between established species it has relatively little importance; the primary walls are ecological and morphological. As in most other animal groups, there is usually slight overlapping of the microgeographical ranges, of the ultimate ecological niches, in closely related species; under natural conditions, interspecific display must occur but rarely. Also, even if such display runs its full course, the specific differences of palps and epigyna are probably in most cases effective final barriers.

In the formation of species, display may prove of more importance. As Mayr emphasizes (1947), the growth of geographic isolation is doubtless the essential factor in all species formation. Granting this precedence, it seems likely that cumulative slight differences in display, as in other behavior, often pave the way for final morphological breeding isolation. No one who has been struck, in other animal groups, by display distinctions within a species or subspecies in different parts of its range can doubt that functional change tends to precede structural differentiation. To give examples from my own experience, a crab and a bird may be mentioned. The waving rhythm of the fiddler, *Uca pugnax rapax* (Smith), varies from Porto Rico down through the islands to Trinidad and British Guiana, and on west through Venezuela to reach a peak of complexity in Cartagena, Colombia. Similarly, the choruses of chachalacas, *Ortalis ruficauda* (Jard.), when heard in Tobago and Caracas, sound as distinct as the calls of ducks and turkeys in a barnyard. The apparent display differences in *Maevia vittata* in Wisconsin and Connecticut (Peckham, 1889, p. 53; Painter, 1913, p. 634) hint at similar geographic distinctions, of obvious evolutionary interest, among salticid spiders.

## X. SUMMARY.

(See also sectional summaries on pp. 184, 185, 187, 190, 192 and 196-199).

1. A study was made of the epigamic display behavior of fifteen species of salticid spiders distributed through seven subfamilies. All observations and experiments were made at Rancho Grande, Parque Nacional de Aragua, Venezuela.

2. The factors comprising the innate releasing mechanisms prove to be similar throughout the family, but their relative importance varies from genus to genus even within the same subfamily, and, in minor sign stimuli, from species to species.

3. The principal controlling factors of the internal releasing mechanism appear to be age, fluctuating epigamic rhythm, hunger, thirst, fatigue, overstimulation and attention.

4. The epigamic rhythm plays an especially important part in daily responses. Only spiders of the highest tone (i.e., lowest epigamic threshold) usually carry courtship to completion in either field or laboratory. No regular periodicity, however, was observed.

5. The controlling factors of the external releasing and directive mechanisms are divided into those of the physical enviroment and of the configurational stimulus situation (sign stimuli).

6. Temperature, humidity and light are recognized as the principal environmental variables. Display may be released throughout a wide range of these factors.

7. Tactile, chemical and visual stimuli are regarded as the major components of the configurational stimulus situation.

8. Display cannot be released through touch, although it plays an important role in the final stages of courtship.

9. Neither is display released through chemical stimuli alone although, in the presence of certain visual stimuli, they are important secondary releasers of courtship. They appear to stimulate two overlapping senses, contact chemoperception (chemotaxis) and distance or airborne chemoperception (apparently akin to odor). The importance of each type, both in comparison with each other and with visual stimuli, depends on the degree of visual dominance of the genus; in the more primitive genera, although they too are visually dominated, greater dependence is placed on chemical senses than in more advanced forms. Absence of chemical stimuli sometimes changes courtship to threat display or actual fighting.

10. Visual stimuli alone are sufficient to release display. The principal factors of the visual stimulus situation appear to be motion, distance, size, form, pattern, intensity and color. The relative importance as well as the characteristics of these factors varies throughout the family, and no single one ever proved to be an essential, primary releaser.

11. In general, motion, form and apparent size are the most important factors, and the sign stimuli among these categories in each genus or species may vary within fairly wide limits. Pattern, intensity (except for visibility contrast) and color, on the other hand, have little releasing value. Sometimes, however, a special contrasting or colored marking does act as a definite releaser or director for display. An example is the yellow clypeal band of *C. xanthopa*, which, in combination with an adequate supporting visual configuration, is a releaser for inter-male threat display. An undoubted director is the white sub-basal abdominal band of many females, which acts as a copulation guide. Most clypeal and palp markings, iridescent patches, leg fringes, etc., have no high releasing value, since complete display readily takes place in their absence without strengthening of other elements in the stimulus configuration.

12. This apparent uselessness of epigamic "decorations" does not, of course, mean that they are necessarily lacking in adaptive value for display or that selection has not been acting upon them toward that end. It is merely a further instance of the unequal value of sign stimuli, and of the lack of a lock-key releasing formula: the effective configuration is made up of many small bits; together, they have cumulative releasing, directive or merely excitatory value, but a number may be missing from an individual situation without noticeable effect. To only one dynamic compound element can the term "primary releaser" be applied: this is a unit composed of any of several adequate visual stimuli; very few releasers and directors are of even secondary importance.

13. Evidence is presented that color perception occurs at least in the yellow region; the two tested genera, *Corythalia* and *Phiale*, appear to be insensitive to the red end of the spectrum.

14. All of the components—external and internal—of the innate releasing and directive mechanism form a closely woven, mutually dependent, dynamic whole. When one important part of the normal configuration is weak or absent, reinforcement of another part—including especially high tone in the receptor spider—can bring a complete response: the concept of heterogeneous summation is as important in salticids as in other animal groups.

15. Nevertheless, in the field courtships are usually incomplete when the stimulus configuration is weak in any particular.

16. Although individual spiders, particularly females, sometimes showed slight, temporary idiosyncrasies, display patterns are fixed and instinctive. No evidence at all was found of display learning, imprinting or copying of other species' patterns.

17. Displacement behavior is confined to actions which normally occur in the sexual field.

18. Little evidence has been found of dominance relationships in the vertebrate sense; temporary dominance seems to be due to fluctuating epigamic rhythms.

19. Sociality and home range concepts apply in some species on a primitive level; no defended territories were observed.

20. The functions of courtship in this family are held to be stimulatory with a simultaneous blocking of hunger drives; the concept of "recognition" does not seem to be necessary.

21. The explanations and functions of threat display depend on the phylogenetic position of the genus in reference to chemical dependence. In the apparently most primitive groups, the males take little or no notice of one another; there is neither fighting nor threat display, nor even inter-male courtship; mirror display does not normally occur. In intermediate genera, with greater visual dependence but strong reliance on airborne chemical stimuli, courtship and threat are similar, usually identical in the first stage, and appear to result from the mistaking of males for females, as suggested by Bristowe. When the mistake is "discovered," fighting often results. In the genera with the least dependence on chemical stimuli, however, courtship and threat are distinct, fighting does not occur and mirror display is readily induced. In these forms, and to some extent in the intermediate group, threat display seems clearly to have a stimulatory function which is totally apart from any direct competition for mates, and which is not concerned in territorial defense.

22. A tentative hypothetical phylogeny is presented, in which the studied genera and some northern relations are placed according to dependence on chemical stimuli, display criteria and method of locomotion. The correlation with morphological characters, to be specially treated in a subsequent paper, are indicated. The evolutionary trend within all the subfamilies appears to be similar in various major characteristics.

23. The origins of most display movements appear to be in accordance with the principle of economical permutation, since the majority probably developed from ordinary motions connected with daily activity.

24. Atavistic behavior was noted in which low-tone, overstimulated or senile individuals of advanced genera resorted to inappropriate aggression and chemotaxis; this was strikingly similar to the normal behavior of more primitive groups.

25. It is held that in salticids, the display motions probably preceded most morphological secondary sexual characteristics, and that the latter often persist vestigially after they have ceased to function as part of the display stimulus configuration.

26. In salticids, as in other groups, sexual dimorphism may occur in all degrees within a closely related group, even within the same genus, and appears to hold little phylogenetic significance. In species having both sexes strongly and similarly marked, the females are often more aggressive than usual and tend to perform definite reciprocal or mutual displays.

27. It is suggested that tropical salticids may differ in behavior from northern forms because of the prolonged breeding season, which necessitates less close correlation of breeding rhythms between the sexes.

28. Although it is agreed that geographic isolation is the prime essential of species formation, it appears that growing display differences may be a strong secondary factor in salticid speciation. As a barrier between species already established, however, display seems to be an effective, but usually supernumerary, isolating mechanism.

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## EXPLANATION OF THE PLATE.

### PLATE I.

FIG. 1. *Plexippus paykullii*. Courtship, Stage II. Typical of Stage II courtship in the Salticidae. In this family, specialization of display occurs principally in the earlier phases.

FIG. 2. Observation table at Rancho Grande, showing presentation of a dried spider to a test salticid. The spider is mounted on an L-shaped strip of pasteboard. The table is covered with oilcloth ruled in concentric circles for distance observations. When chemotaxis was to be eliminated, fresh sheets of paper were used in each test.

FIG. 1.

FIG. 2.

COMPARATIVE BIOLOGY OF SALTICID SPIDERS AT RANCHO GRANDE, VENEZUELA.
PART IV. AN ANALYSIS OF DISPLAY.

# 18.

## Differential Effects of Estradiol, Estradiol Benzoate and Pregneninolone on *Platypoecilus maculatus.*

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(Plates I-V; Text-figures 1-5).

Androgenic effects of estrogens have thus far been described as affecting only secondary sex organs in mammals (Allen, Hisaw and Gardner, 1939; and Witschi, 1939). In the present work, data are presented to show gonodal stimulation and androgenic effects of an estrogen in the platyfish.

The platyfish, *Platypoecilus maculatus* Günther, is a viviparous cyprinodont belonging to the family Poeciliidae. It has been used frequently for genetic studies (Bellamy, 1928 and 1933; Fraser and Gordon, 1929; Gordon, 1927, 1931, 1937a, 1947a and b), for studies of melanoma (Gordon, 1937b, 1948a; Gordon and Flathman, 1943; Levine and Gordon, 1946), and for embryological studies (Tavolga and Rugh, 1947), but until 1940 it was not used as an experimental animal for endocrinological work.

In 1941, Cohen, Gordon and Nigrelli reported on the spontaneous development of gonopodia in females of *Platypoecilus*, while in 1940 and 1942 Grobstein worked out the development of, and endocrine effects on, gonopodium differentiation. Cohen in 1942 and 1946 did the first work on the effects of sex hormones on the platyfish. At that time he found that pregneninolone has an androgenic effect upon the gonads and anal fins of the fish and that alpha estradiol benzoate has feminizing effects on the male. Pregneninolone, in mammals, has been known as a progestogen, although its effects have been discredited in recent years as ineffective and partially androgenic (Corner, 1942; Freed, 1942 and 1943). As above indicated, it has been found since that time that on lower vertebrates, such as fishes, the hormone has an entirely androgenic effect. In experiments preliminary to the present work, it was found that the effects of free estradiol did not coincide with those produced by the benzoate ester, and it was decided to continue and expand this aspect of the work as well as to determine the effects of androgens on the male and estrogens on the female. Pregneninolone was used as an androgen with which to compare the effects of alpha estradiol when it was found that this substance did not exhibit strictly estrogenic activity.

MacBryde *et al.* (1942) found differential effects of estrogenic substances on the mammalian liver. It was decided, therefore, to investigate the effects of the treatment upon the liver of the experimental animals as a possible source of information as to the reason for the differential effects of the two estrogens. With these purposes in mind the present experiments were undertaken.

The author is indebted to Dr. Charles M. Breder, Jr., of the American Museum of Natural History and New York University for his aid and criticism in the progress of the work and in the preparation of the manuscript, to Dr. Myron Gordon of the New York Aquarium of the New York Zoological Society and New York University for his help and criticism during the experiments and for the stock of fishes[2] with which the work was carried out, and to Dr. Lester R. Aronson of the Department of Animal Behavior of the American Museum of Natural History for his generosity in supplying equipment and laboratory space. Thanks are due also to Dr. Robert Gaunt of Syracuse University, who provided the initial stimulus for the problem, and to Dr. Milan J. Kopac of New York University and Dr. Irwin Schwenk of Schering Corporation for obtaining the initial supply of alpha estradiol benzoate.

### MATERIALS AND METHODS.

The fishes used for these experiments were platyfish, *Platypoecilus maculatus*, of the New York Zoological Society's Genetics Laboratory Culture 180 (Gordon, 1948b), their immediate offspring and those of several subsequent inbred generations. In this strain the males are the heterogametic sex (XY). The Y chromosome carries the "spotted" gene (*Sp*), regularly transmitted from father to son when a spotted male $(X)+/(Y)_{Sp}$ is mated to the recessive female $(X)+/(X)+$. The effect of the *Sp* gene is such that

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[2] These animals were obtained from the Genetics Laboratory of the New York Aquarium, New York Zoological Society. The work of this laboratory is supported by a research grant from the National Cancer Institute of the National Institute of Health, U. S. Public Health Service.

groups of macromelanophores are distributed over the major part of the body. The pigment cells begin to show immediately after the birth of the animals, affording a convenient method of identifying males and females within a day or two after birth. The females carry the recessive gene for macromelanophores (+ or *sp*) and appear as gray. In other strains of the platyfish which do not possess this or a similar feature, sex identification is delayed until such time as the fish mature, when the anal fin of the male is transformed into an "intromittent" organ, the gonopodium. Experiments carried out on such fish necessitate knowledge of the ratio of males to females usually derived in a brood from these fish and the use of statistical methods in determining the deviation from such a ratio when the work involves the use of hormones which produce effects on primary and secondary sex organs. This type of analysis is unnecessary with the strain used.

In seven generations only one crossover occurred, and this was in the control group. An animal in that group appeared to be a normal female 21 mm. long, but on sectioning she was found to possess normal testes for a fish of that age (66 days). Fraser and Gordon (1929) indicated that crossing over of the sex chromosomes in the platyfish is likely to occur at the rate of 1%.

The experimental individuals were kept in two-gallon tanks, approximately eight immature specimens of both sexes to a tank. Plants and gravel were removed at the beginning of each experiment in order to secure more uniform conditions. The room in which the tanks were kept was maintained constantly at a temperature of 80° F., plus or minus 3°.

The fish were fed daily on a fresh liver-Pablum mixture (Gordon, 1943) in amounts such that each tank received approximately 1.5 cc. per week. The method of introduction of hormones received a considerable amount of attention. The literature contains accounts of hormone administration both by dropping hormones into the water and by injection (Berkowitz, 1937; Eversole, 1941; Grobstein, 1942a). It was felt that the animals used in these experiments were too small to receive injections, since at the beginning of treatment they were only two to ten days old and averaged only 8 mm. in length. Therefore, dropping powdered hormone into the tanks was attempted.

It was soon noted, however, that the animals learned early to distinguish between food and hormone. At first they ingested it freely, but after a day or two they were observed to ignore it completely and the powder settled to the bottom of the tank, where it remained until removed. Thus the greater part of the hormone was not utilized. The possibility that it may have dissolved and been absorbed was not overlooked, and experiments designed to check this possibility will be discussed later. However, since the solubility of the hormones is known to be relatively small, another method of more direct administration was attempted, and was found to give good results.

The powdered hormone was introduced into the semisolid liver-Pablum paste and thoroughly mixed. The food was given in small lumps each day and the fish were observed to pick at and ingest it freely each time it was given for the duration of the experiment. They consumed the amount given in about twenty minutes and close observation showed that they did not reject any part of the food, nor could any be seen at the bottom of the tank when later observed. Because of this it was assumed that the entire amount was ingested, and with it all the hormone which did not dissolve in the twenty-minute period which was needed for ingestion. Although no accurate measurement could be made of the amount taken in by any individual fish, it was seen that all the fish had access to the food and that there was little fighting among them for it. Each animal, therefore, received approximately the same amount of food and of the hormone. The hormone in oil preparation was mixed into the liver paste in the same manner, and though it changed the consistency of the paste to a slight degree, the preparation which was chosen contained a high concentration of hormone per cubic centimeter and little of the solution was needed to secure the necessary concentration in the food.

The hormones used were pregneninolone (Pranone, Schering), alpha estradiol (Progynon DH, Schering), and alpha estradiol benzoate (Progynon B, Schering). The first two were prepared in tablet form. The initial supply of estradiol benzoate was in powder form and the remainder in solution in sesame oil. The two forms of estradiol benzoate produced indistinguishable results and so are considered together.

The amounts of hormone used were selected in an attempt to secure doses which would be adequate to gain results and at the same time avoid much of the toxicity which was found to occur, especially from pregneninolone (see Text-fig. 1). Pregneninolone was used in doses of 5, 2.5, 1.25 and 0.625 mg. per 3 cc. of food. Estradiol and the crystalline estradiol benzoate were used in doses of 0.5, 0.25, 0.13 and 0.06 mg. per 3 cc. of food. The estradiol benzoate in oil was obtained in ampules containing 1000 rat units per cubic centimeter of solution in sesame oil, corresponding to 0.166 mg., and the doses given per 3 cc. of food measured 0.166, 0.083, 0.0415 and 0.0275 mg. These dosages were obtained by mixing 1, ½, ¼, etc. cc. of the solution or the same fraction of tablets with 3 cc. of food.

Control tanks containing littermates of the experimental animals were run simultaneously with each experiment. In experiments where oil solution of estradiol benzoate was used, tanks of littermates which were fed with a mixture of food and sesame oil alone were also used.

The doses were given for various intervals,

varying from ten days to seven weeks, and at the end of each interval at least one male and one female were removed from each experimental tank and from the control tank. They were immediately fixed in Bouin's picro-formol and preserved after fixation in 70% alcohol. Each fish was then prepared for further study as follows: the anal fin or gonopodium was removed, cleared and mounted entire, and the belly of each animal was slit to facilitate infiltration of solutions. The animal was decalcified in a nitric acid-phloroglucinol mixture for a period of 24 to 48 hours, depending on the size of the fish, placed in several changes of 70% alcohol to remove the acid, and dehydrated by means of Dioxan. After infiltration in 60-62° paraffin, the anmals were cut at 10 $\mu$ and the sections stained with Harris' haematoxylin and eosin, or with acid fuchsin and aniline blue (modification of Masson trichrome stain).

The sections thus obtained were examined to ascertain the condition of the ovary or testis, and the general condition of the other organs, and the anal fins were examined for signs of structural changes which might indicate a progressive shift toward maleness or femaleness. The sizes of the gonads were determined by measuring the widths of these glands. It was found that while the lengths of the gonads were roughly correlated with the standard length (length from the tip of the snout to the base of the caudal fin) of the animals, the width of the gonad was also correlated with the development and apparent activity of the gland as induced by hormone treatment.

In order to determine size differences between the eggs of the treated animals and those of the controls, one or more widely separated sections of each treated and control animal was subjected to analysis. The sections selected were as widely separated as possible in order to insure that no duplicate measurements could be made on any egg. Except for this consideration, the sections were chosen at random. In each case, 100 eggs were measured in order to obtain a good distribution and a sufficient and representative sample. The means and standard errors of the means were obtained and according to the formulas given by Simpson and Roe (1939) the significance values were calculated. These results are given in Text-fig. 4 and Table IV. In the case of the testes, the same method of analysis was applied to primary spermatocytes , secondary spermatocytes and spermatophores. In addition, an adult control male was sectioned in order to afford a comparison between the testes of the treated young animals and a normal adult testis. The testis of this animal was analyzed in the same manner.

## Results.

Two hundred forty-six animals were used experimentally. Each experimental group contained 26 to 33 animals when finally prepared and sectioned. Since with the dosages used there was no statistical difference between those treated for different periods and with different dosages, the descriptions given will cover all periods of treatment and all dosages, except where otherwise indicated.

*General Considerations.*

As was stated above, the animals ate the hormone-impregnated food freely and there was observed to be no fighting among the members of any tank for greater amounts of food. Each pellet of food was eaten within about twenty minutes of its introduction into the tank, assuring almost complete introduction of the hormone into the animals. It was possible, however, that the hormone might be entering the animals by way of absorption taking place from the amount of hormone which dissolved into the water during the time when the food was present in the tank. In order to establish whether such dissolution took place, and whether, if it did, the dissolved hormone remained in an active state, two experiments were set up.

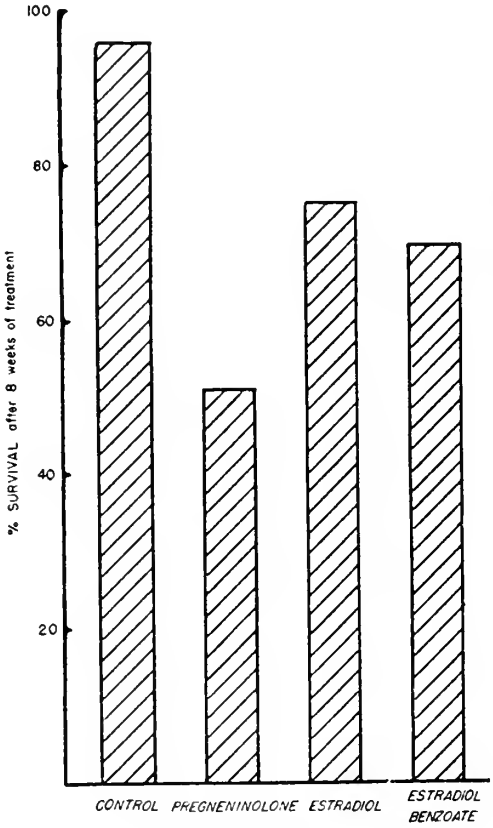
In the first of these, the water between two tanks was circulated through glass wool by a conventional air-lift filter in such a way that the water passed from one tank to the other without any undissolved particles passing in either direction. To the immature fishes of the same strain which were placed in the first tank was fed the same liver-Pablum paste as was used for the main experiments. The fishes in the second tank received the same food without the hormone. The water was transferred from one tank to the other at the rate of about 240 cc. per hour, with a complete turnover at the rate of once in every 30 hours. At the end of a week, the fish in the second tank, which received no hormone in their food, had developed the same effects as those in the first tank which were fed directly, showing, first, that dissolved hormones or their metabolic products affected the animals; second, that dissolution had taken place in an amount great enough to produce an effect on the animals; and third, that the hormone was stable during the time taken for the change of water from one tank to the other.

Three weeks to a month after the termination of the main experiments, immature fish were placed in the tanks used for these experiments without changing the water or washing the tanks. The animals showed no effects of any sort and matured into normal adults, showing that after this period of time the hormone was no longer active.

During the main body of the experiments, the effect of the hormones on the experimental animals was first noticed on the males which were treated with pregneninolone. Within four to five days after treatment was begun, when the animals were six to fifteen days old, and measured 8 to 9 mm. in length, each animal's anal fin was modified into the general form of a gonopodium. A few days later, the anal fins of the females in the same

tanks had also acquired this characteristic. At about the same time (ten to twelve days), the males in the estradiol tanks developed the same type of modification, also followed in a few days by the females. Note that the estradiol, while it had superficially the same effect, was delayed in its action in comparison to the pregneninolone. Those fish in the tanks treated with estradiol benzoate, both males and females, for the duration of experimentation never developed any structures even superficially resembling a gonopodium. That the gonopodia developed by the androgen-treated animals were not typical nor perfect gonopodia with the characteristic hooks, spines, serrae, etc., of the platyfish gonopodium will be discussed later. It should be said here, however, that they were modified in the male direction sufficiently to be considered greatly affected by the hormone treatment, and that the fins of the pregneninolone- and estradiol-treated animals reacted in the same general manner.

Pregneninolone in the amounts given had a serious effect on the viability of the treated animals (see Text-fig. 1). Forty-eight percent. (32) of these animals died before the termination of the experiment and therefore were not considered in the results given. It is believed, however, that this death rate must be a significant consideration in the general effect of the hormone on the metabolism of the animals, and should therefore be included in the general results. The effect of estradiol was similar, but again quantitatively less, as only 24% (17) of the animals treated in this manner succumbed. This number was significant as compared to the death rate of the control, where there was only 4% mortality, but not as compared to the estradiol benzoate-treated group, since 30% (20) of the estradiol benzoate-treated animals also died.




TEXT-FIG. 1. Percentage survival of control and treated animals over a period of eight weeks.

The locomotor activity of the treated animals was not impaired in any way. Sexual activity, normally absent at this stage of development, appeared precociously, and the tiny animals with miniature gonopodia were seen vigorously following the females, in a manner suggestive of precopulatory behavior of adults, as early as one week after the beginning of treatment, when they were but two weeks of age. This type of activity continued until the end of the experimental period. The females of the group, although they exhibited the male type of behavior, showed it to a lesser degree. Although they tended to follow each other, they did so less often and less vigorously. Females were not seen following males. In the estradiol benzoate tanks there was no evidence of male behavior during the entire course of the experiment on the part of either males or females.

*Effect on Gonads.*

Control Males.

All animals in the experiments were young healthy specimens, ranging in size at the end of the experimental period from 8 mm. for those treated for one week to 22 mm. for those treated for seven weeks. None of the animals at the end of the experiments were old enough to be normally sexually mature, and they would not normally have become so for about two months, as *Platypoecilus maculatus* matures at the age of about four to six months under the laboratory conditions maintained here. At the ages of one to seven weeks, therefore, the testes were small compact masses, fused but showing their primary bilobed nature, their anterior ends appearing between two coils of the intestine at approximately the same cross sectional level as the caudal tip of the liver. They were attached to the dorsal peritoneum by a short mesorchium and in a few cases were seen dorsal to the intestines. See Pl. I, Fig. 1. They ranged in width from 0.08 mm. for the smallest animals (7.0 mm.) to 0.35 mm. for the larger ones (19.0-21.0 mm.). The younger gonads could be seen to contain numerous groups of cells (cysts) which could be only poorly differentiated from the main mass of tissue, except under the higher powers of magnification at which they could be seen to be spermatogonia. Between these cysts existed numerous connective tissue cells and fibers, making up the stroma of the gland. The sperm duct in these smaller animals was poorly differentiated. In the larger specimens, none of which was more than eight

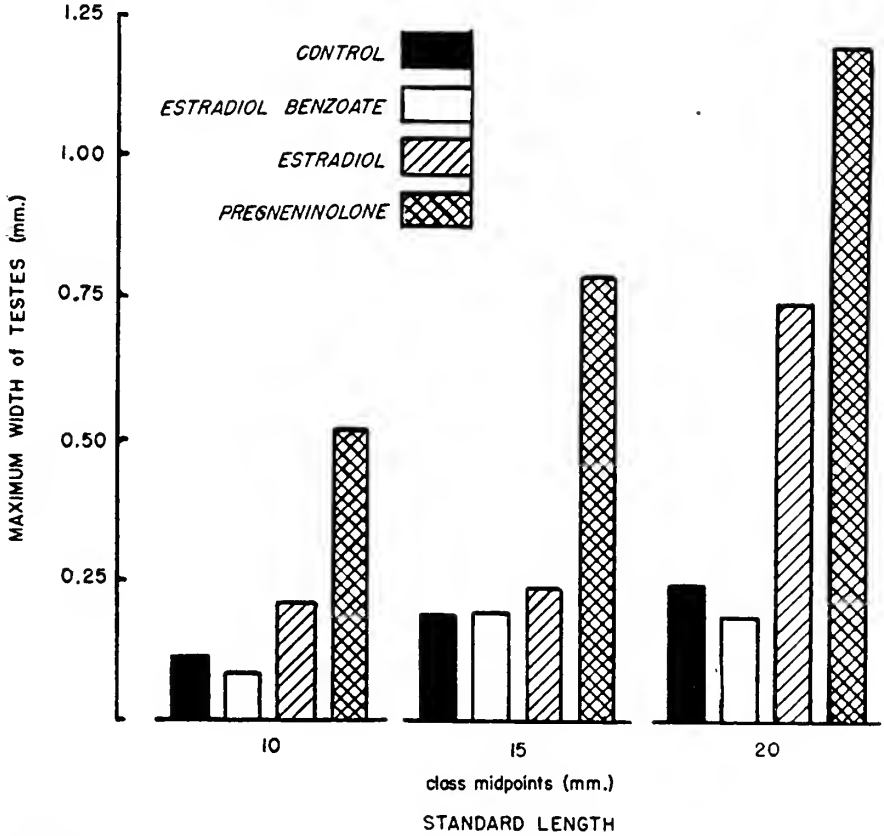
weeks old, the cysts were slightly better differentiated. They could be seen to be separated from their surrounding stroma, which was less distinct, and the smaller cysts had now taken up a position relatively peripheral. At this stage these cysts measured 20 to 33 μ in width. A few larger cysts, 36 to 46 μ in width, could be seen toward the center of the gland. These, under higher magnification, could be seen to be primary spermatocytes. These cysts, when present, surrounded the now well formed duct. These descriptions confirm those of Wolf (1931) on the development of the testis in *Platypoecilus maculatus* at this stage. In no case did the gonads contain any cellular formations acceptable as secondary spermatocytes, spermatids, mature sperm or spermatophores.

Males Treated with Alpha Estradiol Benzoate.

The testes of these animals showed a slightly retarded development as compared with the controls (see Pl. I, Fig. 2). Their size range was equal to that of the normals (0.10-0.34 mm.). The mean was 0.19 mm. The two testes were slightly separated, indicating an inhibition of their development toward a fused gland. The gland in general consisted of a number of peripheral cysts, surrounding stroma cells which were abundant and ducts which were slightly less well formed than the normal. The cysts measured 11 to 21 μ in width, but since the testes were so small there were not enough of them to justify a statistical analysis. A few larger cysts were present, but they were less distinctly demarcated than those of the control. There were no statistically significant differences between the widths of the testes of this group and those of the controls (P = .05—see Table II).

Males Treated with Pregneninolone.

Pregneninolone has been shown to have androgenic activity in the guppy by Eversole (1941) and in the platyfish by Cohen (1946). It was expected, therefore, that it would have a similar effect here. That expectation was justified. The testes of even the smallest of the males thus treated showed definite stimulation effects. These testes were significantly larger than those of the control (P = .001), measuring from 0.36 to 1.50 mm., with a mean of 0.81 mm. (see Text-fig. 2 and Table II). In each case, whether the animal was treated for a short period or a long one, the results were the same except for the general size of the gland, which had sufficient time to grow larger in the animals which were treated for a longer period. The cellular effects, in




TEXT-FIG. 2. Growth of control and hormone-treated male gonads as determined by measurements of testis widths.

TABLE I.

Comparative Sizes of Gonads in Treated and Control Females.

| Treatment | Number of animals | Mean length | Range | Mean gonad width | Extremes |
|---|---|---|---|---|---|
| Control | 13 | 13 mm. | 8-19 | 0.42 mm. | 0.11-1.40 |
| Estradiol benzoate | 13 | 17 mm. | 8-24 | 0.31 mm. | 0.11-0.61 |
| Pregneninolone | 12 | 16 mm. | 13-23 | 0.45 mm. | 0.30-0.85 |
| Estradiol | 16 | 16 mm. | 13-23 | 0.45 mm. | 0.20-0.88 |

every case, were the same. The effect was to stimulate the testes to maturity far ahead of the time at which it would ordinarily be functional. Cysts of spermatogonia were present, measuring 30 to 51 μ in width, but in all the animals of the group the spermatogenic process had gone far beyond the stage of spermatogonia and primary spermatocytes into secondary spermatocytes, spermatids and spermatophores, the presence of which is the usual sign of a functional gland (see Pl. I, Fig. 3). The groups of cells had become differentiated into cysts of maturing primary spermatocytes measuring 93 μ plus or minus 2.1 (see Table III), secondary spermatocytes measuring 97 μ plus or minus 1.5, or later stages, each cyst containing only one stage of spermatogenesis, as is found in mature fish. Many of the cysts contained spermatids in the process of growing tails. Others contained nearly mature spermatozoa with heads embedded in Sertoli cells, beginning the formation of the typical ring of the spermatophore. Still others were found (69 μ plus or minus 1.5 μ) which possessed the completed ring form of the spermatophore, containing mature spermatozoa, tails inward, dark heads forming a ring and massed together. In many cases the released spermatophores were found in the ducts, which is typical of the testis of the mature fish. In all the cases spermatogenesis was active in all its stages; there was an abundance of every stage from the earliest spermatogonia to spermatophores. In a general way the progress of spermatogenesis was from the outer portion of the gland inward toward the duct, and spermatogonial cysts were found mainly at the periphery progressing through primary and secondary spermatocytes to spermatids and spermatophores which were located near the center of the gland and adjacent to the ducts. Since the animals were not treated for more than seven weeks, it is possible that the maximum effects were not obtained. Exhaustion effects in *Lebistes*, in which all spermatogenesis is in very late stages and no spermatogonia are present (Eversole, 1941), were not found. It is possible, therefore, that a longer treatment would have produced glands showing lack of germinal elements such as those described by him.

The position of the glands was also different in the treated fish. In the controls at this age they tended to be placed, as stated before, between the coils of the intestine, and only rarely were situated dorsal to this general position. In the pregneninolone-treated animals, however, the testes had grown so large that they pushed dorsally. They often occupied a position completely dorsal to that of the normal gonad, while in all other cases at least part of the gland projected above the coils of the intestine in cross section. Often they occupied the major part of the body cavity.

The interstitial tissue had also changed. In comparison to the size of the treated gland it was very sparse, being seen as mere threads between the cysts of maturing germ cells. However, toward the center of the gland, where it filled in spaces between the cysts and the sperm duct, slightly more abundant interstitial tissue was often seen. In the main it appeared like connective tissue, often with large oval cells. A few collecting tubules lined with cuboidal epithelium could also be seen.

TABLE II.

Comparative Sizes of Gonads of Treated and Control Males.

| Treatment | Number of animals | Mean length | Range | Mean gonad width | Mean W/SL* | t | P |
|---|---|---|---|---|---|---|---|
| Control | 13 | 15.1 mm. | 7.0-21.0 | 0.20 | 0.0122 | | |
| Estradiol benzoate | 12 | 16.0 mm. | 8.5-21.5 | 0.19 | 0.0125 | .17 | .05 |
| Pregneninolone | 10 | 16.2 mm. | 8.5-21.5 | 0.81 | 0.0518 | 8.9 | .001 |
| Estradiol | 17 | 15.2 mm. | 8.0-22.0 | 0.35 | 0.0209 | 2.4 | .02 |

* W/SL equals the ratio of the gonad width divided by the standard length.

## TABLE III.

Sizes of Spermatogenetic Cysts of Treated and Control Males.

| Treatment | Structure of testis | Number of animals | Sample | Mean diam. (micra) | $\pm \sigma_M$* | General effect |
|---|---|---|---|---|---|---|
| Control at experimental stage | Primary sp. cytes | 14 | | | | Few—insufficient for significant count |
| | secondary sp. cytes | 14 | | | | None present |
| | sp. phores | 14 | | | | None present |
| Control mature male | primary sp. cytes | 1 | 100 | 60 | 1.4 | |
| | secondary sp. cytes | 1 | 100 | 73 | 1.3 | |
| | sp. phores | 1 | 100 | 49 | .9 | |
| Estradiol benzoate | primary sp. cytes | 12 | | | | Very few |
| | secondary sp. cytes | 12 | | | | None present |
| | sp. phores | 12 | | | | None present |
| Pregneninolone | primary sp. cytes | 10 | 100 | 93 | 2.1 | Enlarged over mature control |
| | secondary sp. cytes | 10 | 100 | 97 | 1.5 | Enlarged over mature control |
| | sp. phores | 10 | 100 | 69 | 1.5 | Enlarged over mature control |
| Estradiol | primary sp. cytes | 2 | 100 | 56 | 1.4 | Not significantly smaller than control |
| | secondary sp. cytes | 2 | 100 | 56 | 1.1 | Significantly smaller than control |
| | sp. phores | 2 | 100 | 42 | 1.1 | Significantly smaller than control |

Significance Values Calculated from Means in Table III.

Significance values are calculated as the difference between two means divided by the standard error of the difference.

**Primary spermatocytes**

| | Estradiol | Pregneninolone |
|---|---|---|
| Control mature male | 2.0† | 13.0 |
| Pregneninolone | 14.8 | |

**Secondary spermatocytes**

| | Estradiol | Pregneninolone |
|---|---|---|
| Control mature male | 9.9 | 12.1 |
| Pregneninolone | 22.2 | |

**Spermatophores**

| | Estradiol | Pregneninolone |
|---|---|---|
| Control mature male | 5.0 | 11.2 |
| Pregneninolone | 14.6 | |

* $\sigma_M$ equals standard error of the mean.

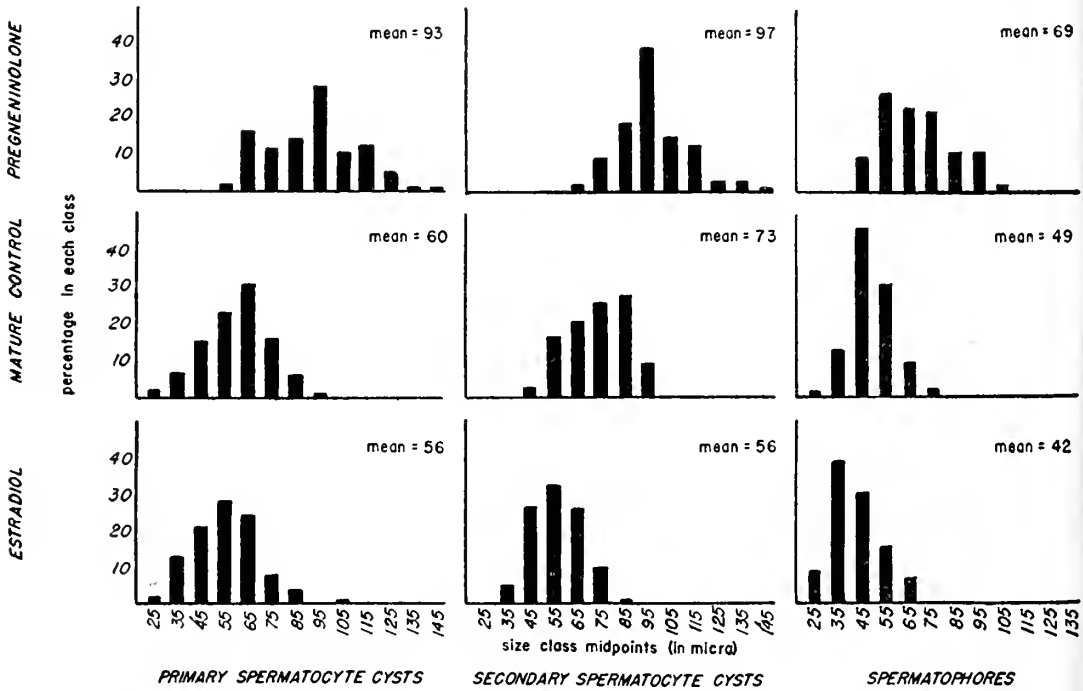
† These values are not to be considered significant.

These observations corresponded very well to Wolf's (1931) description of the interstitium of a young mature male.

Males Treated with Alpha Estradiol.

In mammals it has been found that alpha estradiol is usually an estrogenic hormone (Willier, 1939; Witschi, 1939), although in some cases paradoxical effects have occurred which have affected the secondary sex organs. However, the gonads are not ordinarily changed in these cases. When the present experiments were in their earliest stages, it was found that apparently this was not true in the platyfish. Therefore further experiments were carried out in order to determine the effects of this substance. The animals in this group fell into two sets, the difference being one of size and depending not at all on dosage or length of treatment. In all animals under 18 mm. in length, the testes presented a normal control picture. The testes were small, compact, showed spermatogonia and early spermatocyte stages, compared well in size with those of the controls, except for a very small increase, and generally showed no significant effects. In all animals, however, over 19 mm. in length, the developmental picture was entirely changed. The gonads in these cases were intensely stimulated organs, showing all stages of spermatogenesis. Discrete cysts of primary and secondary spermatocytes, 56 plus or minus 1.4 $\mu$, and 56 plus or minus 1.1 $\mu$, respectively, spermatogonia 25 to 30 $\mu$ at the periphery, and normal spermatophores of 42 plus or minus 1.1 $\mu$ at the center were present. Note that the sizes of these cysts were significantly smaller than those of the pregneninolone animals (see Text-fig. 3 and Table III). The ducts also were large and well formed, typical of the ducts of a mature male, and they were frequently filled with spermatophores. These spermatophores, like those of the pregneninolone-treated animals, were well formed and showed no sign of precocious extrusion from the cysts or of abnormal cells despite their comparatively small size (see Pl. I, Figs. 4 and 5). The picture approximated that of animals treated with the known androgen pregneninolone, in every detail except size. It seems, then, that estradiol, far from being an estrogen, acts much like an androgen in the stimulation of the testes in these fish. The position of the testes in the abdominal cavity of the animal and the appearance presented by the interstitial tissue corresponded in every way to the pregneninolone-treated animals.

In order to determine the size relationship of these stimulated spermatogenic cysts to those of the normal testis, an adult untreated male was sectioned and prepared in the same manner as the experimental animals. As with the experimentals, 100 cysts of each type, primary and secondary spermatocytes and spermatophores, were measured by means of the ocular micrometer and statistical analyses were made (see Table III and Text-fig. 3). In each case the cysts of the pregneninolone-treated animals were significantly larger than those of the adult control and



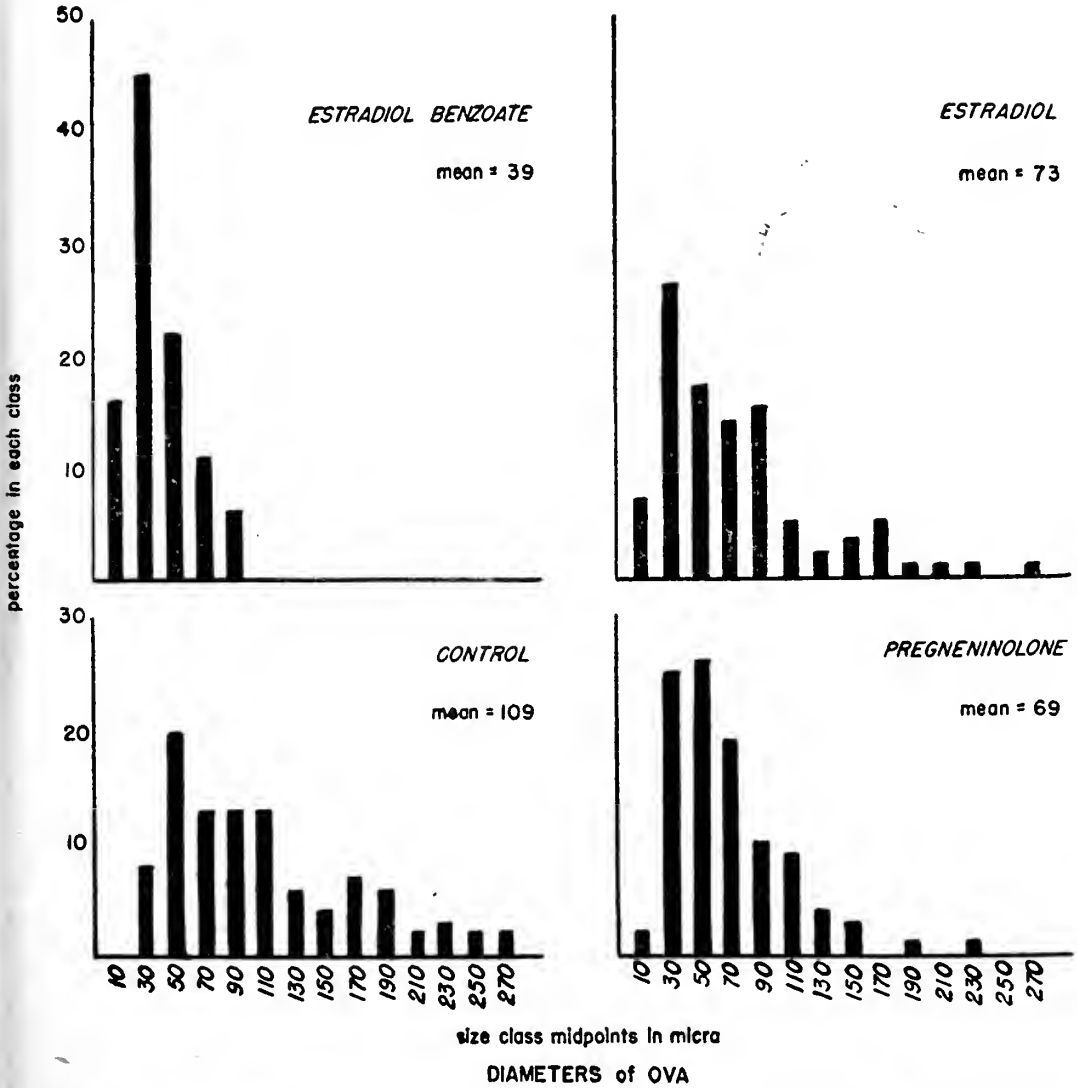

TEXT-FIG. 3. Comparative size ranges of primary and secondary spermatocyte cysts and spermatophore cysts of pregneninolone- and estradiol-treated animals as compared with those of a normal adult male.

with one exception the cysts of the estradiol-treated animals were smaller. In the case of the primary spermatocytes the cysts of the estradiol-treated animals were not significantly smaller than those of the control adult.

Control Females.

The typical female ovary of a platyfish of two to eight weeks of age was located in serial cross sections between two coils of the intestine, suspended from and approximating the dorsal peritoneum. The ovary ranged in size from 0.11 to 1.40 mm. and the mean value was 0.42 mm. Posteriorly it lay free of contact with surrounding organs, and far posteriorly, just anterior to its posterior margin, it lay almost if not completely free in the abdominal cavity. At the young stages studied here, it consisted of a single mass composed mainly of young circular or ovoid ovocytes, before, or in the larger animals during, the process of yolk deposition. The mean size of these ovocytes was 109 $\mu$ plus or minus 6.5 $\mu$ (see Text-fig. 4 and Table IV). The ovary as a whole was compact, little if any space being present between adjacent eggs. Any space which was present was almost filled with small amounts of stroma. Stroma also filled spaces between the outermost eggs and the peripheral flattened epithelium (see Pl. II, Fig. 6).

In the younger stages the ovocytes were yolk-free, with slightly reticular cytoplasm and a lighter-staining nucleus. Each nucleus contained one or two deeply-staining, prominent nucleoli. The nucleoplasm itself was reticular in appearance, studded with chromatin granules. These larger eggs were located mainly at the periphery of the organ and each was bounded by epithelial cells constituting the follicle. The younger cells, oogonia, 21 to 45 $\mu$ in diameter, were situated




TEXT-FIG. 4. Comparative size ranges and distributions of eggs of control, estradiol benzoate-, pregneninolone- and estradiol-treated females.

TABLE IV.

Sizes of Eggs of Treated and Control Females.

| Treatment | Number of animals | Sample | Mean diam. (micra) | $\pm \sigma_M$ | General effect |
|---|---|---|---|---|---|
| Control | 12 | 100 | 109 | 6.5 | |
| Estradiol benzoate | 13 | 100 | 39 | 2.1 | Great inhibition |
| Pregneninolone | 12 | 100 | 69 | 3.9 | Partial inhibition |
| Estradiol | 16 | 100 | 73 | 4.8 | Partial inhibition |

Significance Values Calculated from Means in Table IV.

| | Control | Estradiol benzoate | Estradiol |
|---|---|---|---|
| Pregneninolone | 5.2 | 6.7 | 0.6* |
| Estradiol | 4.3 | 6.1 | |
| Estradiol benzoate | 10.2 | | |

* These values are not to be considered significant.

nearer the ovarian cavity. They were sometimes imbedded in the stroma immediately surrounding it, but usually maintained contact with the epithelium of the cavity. Their cytoplasm was more deeply stained and presented a more homogeneous appearance.

In the later stage the situation was much the same except for the appearance of the larger eggs. These had now grown considerably in size, measuring 100 to 280 $\mu$, and their cytoplasm presented a far more reticular appearance than was true of the younger eggs. Near the periphery of some of them yolk granules were discerned, but this was true only in the largest of them. In all cases intermediate stages were present between the largest and smallest eggs.

Females Treated with Alpha Estradiol Benzoate.

The ovaries of the animals treated with alpha estradiol benzoate were more compact and smaller than those of the controls, measuring 0.11 to 0.61 mm. and averaging 0.30 mm. in width. The eggs appeared tightly pressed together and were deformed by this pressure in some cases. The ovaries were more closely pressed between the coils of the intestine. Although the arrangement of the eggs appeared normal and a fairly well formed duct was present, the eggs themselves showed an inhibition of development (see Pl. II, Fig. 7). The larger eggs were peripheral, gradating to smaller ones in the center of the organ. In size they ranged from 11 to 96 $\mu$ (see Text-fig. 4 and Table IV), and none of them approached the size of eggs found in the control fishes of the same size. No evidence of yolk deposition was present in any of the eggs in this group. The cytoplasm of these eggs was more homogeneous than was true of the ova of the controls, and they compared in size and structure to a much younger stage than that which would be expected from the age and size of the fish. It is evident, then, that though few acute abnormalities were present in the structure of the individual eggs, their size and appearance indicated that they were greatly inhibited by the treatment.

Females Treated with Pregneninolone.

The ovaries of these animals were again slightly smaller than those of the controls, measuring from 0.30 to 0.85 mm. and averaging 0.45 mm. in width. The sizes of the groups overlap a great deal (see Table I), but the largest ovaries of the pregneninolone-treated animals did not reach the size of the largest ovary of the control group. The main effects, however, were those appearing in the size and structure of the eggs. The ovaries of these animals presented an extremely abnormal appearance. The greater number of them were shrunken and small, appearing completely pressed out of shape by the surrounding coils of the intestine, as in the estradiol benzoate-treated animals (see Pl. II, Fig. 8). It is doubtful, however, whether this shrunken appearance was due to the pressure caused by the intestine, since the control ovaries were subjected to the same pressures and did not show the deformities. Also the pregneninolone ovary, like the controls, lay, at its posterior end, free in the abdominal cavity, and the deformities were equally great there. Therefore some other cause must be assigned to this phenomenon, presumably one due to the hormones involved. The ovaries contained in most cases little interstitial tissue, and while this was more deeply stained than the normal, it did not appear especially abnormal. The eggs themselves, however, showed definite effects. They were seldom as large as those of the control, having a mean size of 69 $\mu$ plus or minus

3.9 $\mu$ (see Text-fig. 4 and Table IV). In a few cases large eggs could be found and these were the most nearly normal-looking ones. Even they appeared degenerate, however, showing deeply-staining cytoplasm, slightly irregular nuclei and a partially deformed appearance. The remaining eggs were uniformly deformed in shape, the main body of them having irregular depressions in their sides and usually one concave side, so that the individual eggs took on the appearance of pushed-in balls. The nuclei were also misshapen, showing elongations and irregularities, each one staining deeply. The cytoplasm often had a mottled appearance, in contrast with the even staining of the control. This resulted, presumably, from some effect on the cytoplasm, which caused parts of it to stain deeply and others lightly, without any regularity. Another significant point was in regard to the size of the eggs. All those which were not included in the groups of larger eggs mentioned first were extremely small as compared to eggs in the same stage of a control, measuring from 11 to 60 $\mu$. No evidence of yolk deposition could be seen in any individual eggs.

In most of these ovaries the duct was poorly formed and the edge of the epithelium was ragged and abnormal, showing cells and bits of tissue sloughing off into the duct.

Two variations of these conditions were found. In two cases the ovary was large but the eggs were scattered and large spaces were present between them (see Pl. II, Fig. 9). While the eggs in these specimens were not usually as deformed as they were in the cases described above, they were deeply stained and appeared to be in a state of degeneration. As above, few eggs could be found which were as large as those of the control of the same age and size, but several appeared which had been approaching this size and condition before treatment with hormones was begun. These eggs showed approximately the same irregularities as the large ones described above. The epithelium surrounding the gland was ragged and shredded in many places and the cells of the duct were ragged.

In two other cases a definite bi-partite ovary was found. In one of these the eggs were fairly large and normal-looking, measuring between 90 and 130 $\mu$ (see Pl. II, Fig. 10), and appeared to be comparable to the eggs of the majority of the control ovaries. In the other case, however, the eggs were small and degenerate-looking, measuring about 40 to 60 $\mu$, and were stained deeply, showing deformities. In this ovary there appeared two definite ducts, one for each half of the gland, which showed fairly regular epithelium. The first case contained a duct which was wide and flat horizontally, apparently serving both sides of the gland. It is believed that this remaining evidence of the bi-lobed nature of the embryonic gonad may have been caused by the inhibitory effects of the androgenic hormone applied. All variations of the ovarian conditions were used together in making the statistical analysis of the eggs in this group.

Females Treated with Alpha Estradiol.

In general terms, the ovaries of this group showed the effects expected of an androgen. The results were very similar to those produced by pregneninolone. The majority of the animals possessed ovaries which appeared as shrunken masses, with deformed eggs such as those described for the pregneninolone-treated animals, staining poorly and in a mottled fashion. The size also, of both the ovaries and the eggs, was comparable to the size of those of a pregneninolone-treated female, since measurements of the ovaries ranged from 0.20 to 0.88 mm. with a mean size of 0.45 mm. (see Table I). The eggs had a mean size of 73 plus or minus 4.8 $\mu$, a size which is not significantly different from that of the pregneninolone-treated eggs.

There were several exceptions to this general picture. In two cases the ovary showed the same scattering which appeared in some of the pregneninolone-treated animals (see Pl. II, Fig. 11). The same larger degenerating eggs, and the same type of atretic appearance in the small eggs was present. In one case, there appeared a bi-lobed ovary such as that described above, which possessed one duct to serve both parts of the gland. In this specimen the eggs were small, measuring 40 to 60 $\mu$, and while not as deformed as the typical eggs of this group, some atypical shapes were present and the eggs generally stained more deeply than the controls. In some cases there appeared a variety of degeneration not seen in the pregneninolone-treated group. In these ovaries there were a few eggs which appeared to be almost normal, both in size and general appearance. The remainder of the comparatively large gland was composed of a substance which at first appeared to be adipose material. Upon closer inspection, however, it was concluded that at the places where this material was seen, there had once been large eggs in the process of yolk deposition (see Pl. II, Fig. 12). The eggs had apparently degenerated, since the masses contained no recognizable structures, and left behind them a mass of fatty yolk-filled material. Vacuoles were present, which showed the presence of lipoids. Some yolk granules were to be seen. At certain points about the periphery of these masses there appeared epithelium of a largely degenerate nature which was broken and sloughed in parts. Since there had been several eggs of this nature, it might have been expected that there would be some type of separation between them. For the most part, however, this was not true, and the masses were indistinguishable from one another, showing no evidence of where one egg ended and another began. In some places a portion of the above-mentioned epithelium remained, to give some indication of the limits of the egg, but this was true only in a few cases. The masses

of material were of various shapes so that no indication remained of the original shape of the ovum. The remaining eggs were of the small deformed type mentioned above and were pushed to one side of the organ. The ovary, because of this peculiar content, was quite large, although the egg content was extremely small. The appearance of the organ as a whole was a degenerate one. The outline of the organ, even where the eggs were present, was ragged and appeared degenerate, as the epithelium was ragged and uneven in contrast to the smooth epithelium of the control.

*Effects on the Anal Fin.*

Grobstein in 1940 published a complete description of the developmental stages in the transformation of the platyfish's anal fin into the gonopodium. In 1942, however, he partially changed the terminology used in order to conform to prevailing taxonomic usage. In all the following descriptions, the terminology used in the 1942b paper will be employed.

Control Males.

The anal fin of the control male fish at the ages studied here was one in which no differentiation or growth had taken place in the change from the undifferentiated fin toward the typical gonopodium. The fin looked like the female fin of the same age (see Pl. III, Fig. 13). The fins were well formed, the third ray slightly thicker than the others. The fourth and fifth rays, particularly the fourth, projected slightly beyond the others. No bifurcations were present in the younger fins and the larger ones possessed only primary bifurcations. Secondary and tertiary bifurcations which, according to Grobstein, depend on age, had not yet appeared in any of the fins studied. No growth of the third ray, which indicates the beginning of differentiation into the gonopodium, had begun in any of the fins. The only difference between the male and female control fins at this age was the presence of macromelanophores in the male fin, due to the *Sp* gene. The females did not possess these macromelanophores.

Males Treated with Alpha Estradiol Benzoate.

Fins of the males treated with alpha estradiol benzoate presented the same picture as did the controls. In all the fins, which came from animals not more than eight weeks old, no differentiation of any sort tending in the male direction was seen. The fourth and fifth rays projected slightly beyond the others, but no more so than is normal in the female fin and certainly not enough to give the impression that they are beginning the gonopodial growth phase (see Pl. III, Fig. 14). They appeared as normal fins for this age of fish, but since no animals were carried to maturity it is not known whether the hormone would have been enough to prevent gonopodial differentiation entirely.

Males Treated with Pregneninolone.

The anal fins of all animals in this group were affected by the hormone treatments. In the case of the smallest animals, ten days to two weeks of age and 8 to 9 mm. in length, which had been treated for one week to ten days, the transformation had proceeded only into Phase I, and all these fins possessed third rays which were segmenting and growing, producing an elongation of the cephalad portion of the fin. All those treated for three weeks or longer, however, showed a completely modified picture. In these groups, every fish possessed an almost completely differentiated gonopodium (see Pl. III, Fig. 15). Most of these were almost perfect, although a few existed which were lacking in certain elements present in a normal fin. The usual element missing in such an incomplete fin was the spines, which in most cases, if present, were flattened and smaller than normal. Some fins were seen where no spines at all were present. Since the oldest fish in the group were not more than eight, or at most, nine weeks old, it can be assumed that this precocious development was due to the effects of the hormones administered. That the modifications of the fins correlated well with the growth and differentiation of the gonads is further evidence for this assumption.

Males Treated with Alpha Estradiol.

Anal fins of males treated with alpha estradiol could be placed in two groups. These corresponded directly to the division which occurred in the description given already of the gonads of this group. In those animals which were below the size of 18 mm. at the end of the experiments, the fins, like the gonads, did not show the usual effect of the androgen. Each of the anal fins observed in this group was in Phase I of growth and elongation of the third ray. The fins appeared as modifications of the female condition in which the third, fourth and fifth rays had grown long enough to project beyond the others to about one-third of their length. In the majority of the animals, the third ray was found to be segmented as in Phase I, rather than like the control, in which segmentation was far less definite.

The group comprising those animals which reached a size of 19 mm. or more contained fins which were modified far more toward the typical male condition. They were almost complete but showed more variability than did the pregneninolone-treated males. Elements which were present consistently were the subterminal segments with the terminal hook, the elongation of the fourth ray, with its cephalic ramus curved in a cephalad direction, spines and proximal serrae. Elements which were absent or incomplete in the imperfect fins were distal serrae, the spoon and spoon support, and the blade. These were absent in different combinations. Although the fins of this group were not complete, they showed a definite tendency toward the male form (see Pl. III, Fig. 16). If,

as Grobstein postulates, the gonopodium is under the control of the testis, the present evidence supports that view.

Control Females.

The anal fin of the female control animals, like the males at this age, showed no signs of differentiation toward the adult form. The structures possessed by these fins were those typical of the young female (see Pl. IV, Fig. 17). The fins did not differ materially from the adult female type except that, as in the male, only primary bifurcations of the fourth to ninth rays had taken place. The third, fourth and fifth rays projected slightly beyond the others, as is normal. The thickening of the third ray present in the male fin at this age was present to a lesser degree in the female. No macromelanophores were present, since the female does not carry the *Sp* gene. Except for this last distinguishing characteristic, present only in this strain, the fins were structurally similar.

Females Treated with Alpha Estradiol Benzoate.

In animals treated with this estrogen, the condition of the anal fin was indistinguishable from that of the control fin (see Pl. IV, Fig. 18). The third, fourth and fifth rays showed the same slight extension. The third ray was again slightly thicker than the others. Bifurcations of the rays in animals of the same age were identical.

Females Treated with Pregneninolone.

The fins of the animals in this group presented a varied picture. None of them possessed a complete and normal gonopodium, but neither did any possess the typical female anal fin. All animals possessed fins which had progressed far beyond the first phase of gonopodium formation and many had gone into the third phase (see Pl. IV, Fig. 19). All animals had completed the preliminary growth phase, in which the 3, 4, 5 ray complex segmented and pushed out in the cephalo-distal portion of the fin to form a promontory there. Elongation of these rays continued throughout Phase II of gonopodium formation. At the beginning of this growth new segments appeared in the third ray, and at the end of the first phase there were generally nine segments present (Grobstein, 1940). During the second phase, these segments increased in number to twenty-two when the gonopodium had completed its growth. All animals in the group possessed at least ten segments and specimens were found in which the complete number was present. At the end of Phase II differentiation of the various specialized parts of the gonopodium began. The great majority of the animals had arrived at this stage. In many, however, the differentiation was aberrant, showing certain completely differentiated parts, while other parts, which should have differentiated concurrently, were still in an undifferentiated or partially differentiated state. Plate IV, Fig. 19, shows a gonopodium of this group in which the differentiation was almost complete. This fin had progressed as far as the "blade stage" (Grobstein) and shows most of the elements of a complete gonopodium in a more or less normal state. The fin possessed proximal and distal serrae, the blade, the spoon and spoon support, the terminal hook and subterminal segments and other elements. Other gonopodia were found which possessed good segmentation of the third ray and a perfect terminal hook, which should not appear until the time at which the distal serrae differentiate and after the formation of the proximal serrae, but both sets of serrae were missing. Such varied differentiations were common but the general rule in this group was partial or complete differentiation of all parts, many with slight deformations.

Females Treated with Alpha Estradiol.

Alpha estradiol was found to have almost the same effects as pregneninolone, although they were somewhat delayed (see Text-fig. 5). Thus the majority of the fins in this group had begun differentiation but had progressed to a lesser degree than those of the previous group. All the fins had entered the first or preliminary growth phase, since all of them showed at least the segmentation and strengthening of the third ray, and the resulting promontory forming on the cephalo-distal border. Most of them had in addition entered the second phase, in which growth had gone on to form a great elongation of the fin. About one-third of them went on into the third phase, in which they showed various stages of differentiation. In this group no complete gonopodia were found, but many fins showed the beginnings of the differentiated elements. There were present terminal hooks together with subterminal segments, proximal serrae, a few sets of distal serrae, the cephalic turning of the fifth ray, and the cephalic ramus of the fourth ray. All these, however, while they appeared together in a few animals, were usually present in less complete combinations. Alpha estradiol, while it is androgenic to a great extent, since it induces the formation of gonopodia, does not produce nearly as complete gonopodial structures as does pregneninolone (see Pl. IV, Fig. 20). The presence of an androgenic effect, however, is easily seen.

*Effects on the Liver.*

Control Animals.

The liver in the platyfish was divided into several large lobes. Lobules were not separated as in the mammal, and the entire gland appeared as a compactly arranged mass of cells. Cords of cells were present, though not as distinctly as in the livers of higher forms. The cells themselves measured about 8 $\mu$ in diameter and were weakly eosinophilic. The nuclei averaged about 2 $\mu$ in diameter. The stroma was poorly distinguished from the epithelial cells. The mass of homogeneous-

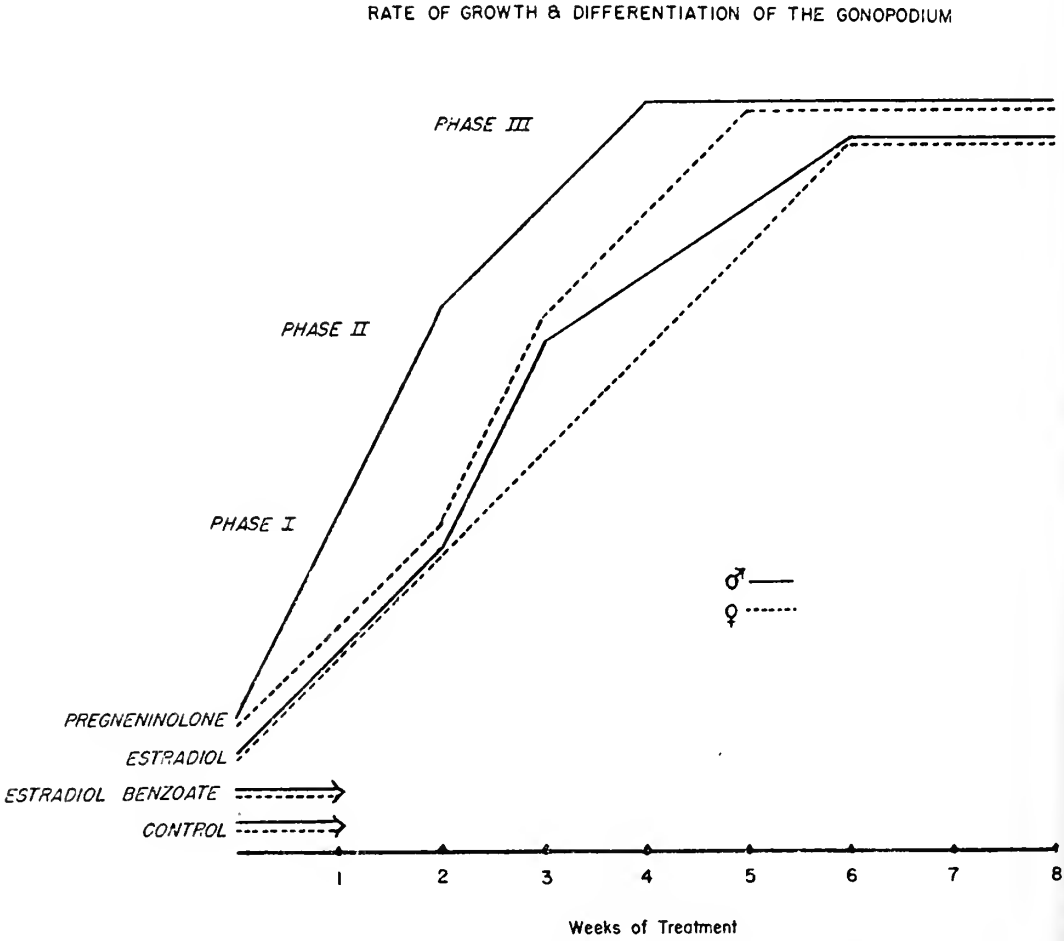
appearing cells was profusely supplied with blood vessels of all sizes. The nuclei, from 2 to 3 $\mu$ in diameter, were nearly circular and thickly granular. The cells were of three types, non-vacuolated with weakly eosinophilic cytoplasm, partially vacuolated with one or two vacuoles filling about one-third of the cytoplasm, and a third type in which larger vacuoles filled most of the cell. In all the vacuolated cells, the vacuolated ends aggregated together in a direction farthest from the blood vessels, producing pale blotches in the structure of the liver from 10 to 20 $\mu$ in diameter and very irregularly placed. The predominant type of cell was the partially vacuolated one. The second cell type in order of predominance was the one which was non-vacuolated and weakly eosinophilic. See Pl. V, Fig. 21.

Animals Treated with
Alpha Estradiol Benzoate.

The liver cells of these animals averaged 8 to 12 $\mu$ in diameter. Three types of cells were present, one non-vacuolated and weakly eosinophilic, another containing a vacuole which filled one-third to two-thirds of the cytoplasm, and a third which was highly vacuolated. The predominant type was that in which one-third to two-thirds of the cytoplasm was vacuolated, followed by the non-vacuolated type. The organ as a whole presented a compact appearance much like that of the control. The stroma network resembled that found in the control. No degenerative effects could be noted. See Pl. V, Fig. 22.

Animals Treated with Pregneninolone.

The cells of the livers of these animals averaged from 10 to 15 $\mu$ in diameter, being generally much larger than those of the control. The cells were all more or less vacuolated. The type of cell which predominated was one in which the cytoplasm was occupied almost completely by a large vacuole. The vacuoles occupied, on the average, about nine-tenths of the cytoplasm and as a direct result the nucleus and remaining cytoplasm were pushed to one side. The general arrangement of the cells about the capillaries was as in the control and the entire organ presented a highly vacuolated appearance (see Pl. V, Fig. 23). Vascularization appeared increased, with a capillary for every




TEXT-FIG. 5. Graph showing growth of gonopodium of control, estradiol benzoate-, pregneninolone- and estradiol-treated animals.

seven to ten cells. The stroma network appeared more distinctly as a result of the extreme vacuolization of the parenchyma cells. The entire organ showed changes in structure, fatty in nature as demonstrated by the application of Sudan IV in frozen sections. The controls used for these reactions were normal livers of the same age, which showed comparatively few sudanophilic globules. The experimental animals, on the other hand, showed an abundance of these globules in their liver cells.

Animals Treated with Alpha Estradiol.

The liver cells in these animals averaged about the same size as those of the estradiol benzoate-treated animals, but the great majority of them showed vacuoles. Occasional cells showed the extreme vacuolization of the pregneninolone-treated livers, nine-tenths of the cell being occupied by a vacuole. For the most part, however, the cells contained vacuoles which occupied about one-half their volume and there appeared frequently cells with several small vacuoles instead of one large one. In general, the organ showed signs of far greater vacuolization than the control, and, therefore, partial changes similar to those shown by the livers of the pregneninolone-treated animals, but in a stage which was far less advanced. See Pl. V, Fig. 24.

## Discussion.

Regnier in 1938 made a comprehensive survey of the history of fishes as experimental animals in sex hormone studies, and in addition described her own experiments on *Xiphophorus hellerii* with anterior pituitary hormones and ovarian and testicular powders and extracts. Essenberg (1926) described sex reversal in *Xiphophorus*. Blacher in 1926 found that testicular hormones are necessary for secondary sex characteristics in *Lebistes*. Castration and implants of gonads in *Xiphophorus* was carried out by van Oordt and van der Maas (1926). Berkowitz, in a series of papers (1937, 1938, 1941a and b), described the effects of estrogens and mammalian gonadotrophins in *Lebistes*, while Eversole (1939 and 1941) worked on the effects of androgens in this animal. In two papers in 1941 (a and b), Turner tested the effects of androgens on *Gambusia*. Scott (1941 and 1944) worked on the effects of steroids on the skeleton of *Lebistes*.

Eversole (1941) mentioned that testes of *Lebistes* treated for 42 days with pregneninolone showed all stages of spermatogenesis, with later stages predominating, that the spermatids and spermatophores produced were abnormal, and that in animals treated for 50 days, later stages in spermatogenesis were present almost exclusively, spermatids and spermatophores were atypical and that the gonad was generally in a degenerate state because of a rapid maturation of the germinal elements which left few spermatogonia. He also stated that the epithelium of the ducts tended to dismember at that time and that the stroma was hypertrophied. These observations were not seen in the present studies. Most of the animals, it is true, were not treated for more than six weeks, but some were treated for seven weeks, and even these did not show the degeneration of the gonad which was described by Eversole. Whether this difference was caused by the difference in experimental animals used, by the different method of administration of the hormone, by differences in dosages or ages, or by different conditions under which the animals were kept, is not clear. However, the gonads of the animals in the present work, while they showed great stimulation, were seen to contain germinal elements and abundant primary and secondary spermatocytes as well as spermatophores. This was true whether the animals were treated for two weeks or for seven. In the case of the animals treated for six to seven weeks, the picture of the gonad was equivalent to a normal mature testis, both in size and in quality of the elements contained. Spermatogonia were present, both primary and secondary spermatocytes were abundant, and the later stages of spermatogenesis were abundant and appeared normal. No signs of degeneration of any sort could be distinguished. As was stated in the results, it is possible that a longer period of treatment might have produced the exhaustion effects spoken of by Eversole.

Winge (1934) has shown that sex reversal may be detected by genetic means in the guppy. These reversals, however, were always from female to male. It is evident, however, that the sex determining mechanism in the guppy is less stable than that of the platyfish, since only two cases of sex reversal in *Platypoecilus* have been mentioned in the literature. Both of these were naturally-occurring phenomena (Breider, 1942; Gordon, 1947a). No sex reversal in the platyfish has ever been reported as having been induced by hormonal or any other means. Because of this relatively unstable sex mechanism in the guppy, it is easier to understand why Berkowitz (1937) was able to secure sex reversal and ovotestes in this form. No such phenomena were found in the present work. Although degeneration of the gonads was common as a result of hormone introduction, no sign of any transformation in the gonads was obtainable, either from male to female, or from female to male.

Berkowitz (1937, 1938, 1941), in work on the guppy, mentioned several hormones and combinations of these which were administered, and combined the results into a general statement. It is possible, therefore, that the divergent results of one or more of the hormones given by him went unnoticed because of this procedure. Although the results appear to be consistent, no mention is made of exactly which results were occasioned by which hormone and slight differences which might have led to a suspicion of the present findings might have been overlooked. A re-

grettable tendency evident in many papers is to administer "estrogens" without regard to which estrogen is being administered. The present work indicates that such a procedure is not safe.

Essenberg in 1923 stated that the oviduct in *Xiphophorus* was derived from a fusion of the two embryonic components of the ovary in such a way as to leave a space between them which later developed into the oviduct. Wolf (1931), on the other hand, who worked out the embryology of the gonads in the platyfish, stated that the oviduct originated by what may be considered the classical method, the degeneration of the medulla of each embryonic gonad accompanied by the development of the cortex (Willier, 1939). Goodrich *et al.* (1934) found that the oviduct of the guppy originated in the same way. Two such opposing views in two forms which are comparatively closely related seems to be unusual. Evidence for the double origin of the oviduct, in which the duct develops in two parts, one in each embryonic ovary, fusing to form one duct when the ovary itself fuses (Wolf's version), is given by the occurrence of the degenerate ovary under androgen treatment found in this work which possessed two distinct ducts. Such a condition, under the terms of Essenberg's hypothesis, would be unlikely. A further investigation into the origin of the oviduct in *Xiphophorus* would seem to be in order.

Regnier (1938), in her description of the origin of the oviduct in *Xiphophorus*, quoted Essenberg, but since this phase of her work was a review of the literature, no further evidence was to be found there. Regnier mentioned the effects of testis powder as producing bi-lobed and retarded ovaries in *Xiphophorus* when these animals were treated when very young. She also mentioned the comparatively great mortality present when this treatment was given, but said that with the addition of anterior pituitary lobe powder to the water in which treated individuals were placed, the mortality markedly decreased. After injections of testosterone for two months, her animals showed mature sperm in the testes, but no mention is made of presence or absence of spermatophores. Therefore it is not known whether the treated males in that group were fertile. She also discussed sex reversal due to hormones and the prevention of sex reversal by injections of appropriate hormones, but since it is known that the sex determining mechanisms of *Xiphophorus* are somewhat labile (Essenberg, 1926; Witschi, 1939), these results are not inconsistent. Mention was made of certain residual bodies which were derived from the degenerating follicles of the sex reversing ovaries and which traveled to nearby organs where they established themselves. Although evidence of such bodies was sought in the surrounding organs of the fish in the present work, no results were obtained.

Cohen in 1942 and 1946 treated female platyfish with pregneninolone and males with estradiol benzoate. He found at that time that estradiol benzoate had feminizing effects on the male platyfish over a twelve-week period. The other results produced were similar to those found in the present experiments within the time limits used here, except that Cohen showed evidence that mature ova were found in normal control ovaries of fishes only eight weeks old. In the entire group of control females used in the present work, only one such ovary was found. This lack of yolk-filled eggs in the ovaries was not considered unusual, since, although growth rates vary with environment, feeding and other factors, *Platypoecilus*, even under ideal conditions, does not usually mature until the end of the fourth month after birth or later, as will be shown. Under normal conditions, no mature ova would be expected to occur until or just before that time. The effects of pregneninolone which were repeated in the present experiments were in the main more pronounced than those shown in Cohen's work, probably because of the larger amount of hormone actually introduced into the fish as a result of the different method of administration used here. It is believed that this method has been more effective, since the main portion of the hormone was introduced into the fish orally. However, the experiments run subsequently show that some of the drug was dissolved into the water, either during the time when the food lay at the bottom of the tank or after it was egested or excreted by the fish in a still potent state. That these drugs affected the fish within a short time, through whatever means they became dissolved, is also evident. The evidence brought out by the later experiment showed, however, that the hormones are not stable under aquarium conditions for more than about three weeks, since after that time immature fish introduced into the tanks with the same water showed no effects whatsoever. Whether the hormone was destroyed by the microscopic population of the tank, adsorbed to the glass, or otherwise inactivated in some way is not known, but after that time it was no longer present in a form which had any perceivable effect on the fish. Further work is being done to determine the exact time when this inactivation takes place, and also, if possible, what the cause for the inactivation may be.

As to the effects of estradiol benzoate on the male, Cohen showed no figures on the development of either the control or the treated testes for eight-week-old fish, and therefore it is difficult to compare results at that age. In the present work, however, the testes so treated were slightly retarded in differentiation though not in size because of the administration of the hormone. Whether these effects are similar to those found by Cohen for an eight-week period is difficult to judge, because his descriptions did not cover that period.

Some support for the theory that different esters of the same hormone may bring about

different effects was given by Grobstein (1942b), when he found that different esters of testosterone may show different effects on the regenerating anal fin of the platyfish. Even this paper, though, showed that all the esters used produced masculinization of the fin, as might have been expected. That a hormone and its ester should bring about diametrically opposed effects is unique. Grobstein also showed that the effects of these hormones is not to produce a normal gonopodium, but one that is imperfect. That evidence is substantiated here. In all cases there was produced a fin which was not precisely like the typical male gonopodium as it is seen in a normal adult animal. Even in those cases where the differentiated parts appeared to be almost normal, two differences in size were noted. The fin as a whole was smaller than the normal, and within this smaller fin the proportions existing between the length and width of the fin were changed. The 3, 4, 5 ray complex in each smaller fin was approximately one-third shorter than would normally have been found in a fin of the same width. The cause of this difference is apparently the result of differentiation of the fin beginning before it had time to grow to its full length, because of the relatively rapid action of the hormone. In the normal fish, the testis develops more slowly and therefore apparently controls the fin in such a way as to produce a lower amount of hormone until the fin has reached its maximum length, at which time the testis releases more hormone and differentiation takes place. This theory of hormone levels controlling the growth and differentiation patterns was postulated by Turner (1941b) and was adopted by Grobstein.

It should be established that under normal developmental conditions the young fish involved in these experiments would not have matured for about two months after the termination of the treatment, since they mature at approximately four to six months of age. Littermates of the experimental animals matured under conditions equivalent to those used in the experiments within these time limits, and averaged five months from birth to sexual maturity.

It can be assumed that a testis may be considered functional when it is producing spermatophores. Although no correlation has been found as yet to support this assumption in hormone-treated animals, it is always found that a normal functional male possesses spermatophores, while a non-functional male, otherwise normal, or an immature male, does not. Because of this evidence, it is assumed that the testes of the animals treated with pregneninolone, and the larger animals treated with estradiol were functional. Even if free sperm are produced under experimental conditions, the fish will not be sexually functional because of the necessity for transferring the sperm in a clump from the gonopodium of the male to the vent of the female. If this transfer is not carried out by way of the spermatophore, the sperm will presumably be lost in the water and fertilization will not result. Therefore, the important feature of the pregneninolone-treated testes was the large number of spermatophores present in both the acini and the duct. Since the normal testis at this age shows none of these features, the indication is that a great stimulation had occurred. Another feature to be mentioned is the difference in reaction of fish of the same age and size to the two hormones which produced stimulation of the testes. In the case of pregneninolone, the stimulation was a steady one, producing in every fish some sign of stimulation, the amount of growth and differentiation depending on the size and age of the fish. It was, however, never completely without effect. This may be seen from the sizes of the testes shown in Text-fig. 2 and Table II. Alpha estradiol, on the other hand, produces quite a different effect. In all the small fish, those below and including 18 mm., the effect was negligible. The testes appeared like normal control testes of the same age. When, however, the fish reached the size of 19 mm., the effect was different. The testes of the fishes of this size were immediately and greatly stimulated (see Pl. I, Figs. 4 and 5), and the testes resulting appeared to be functional, considering the great number of spermatophores present in the acini and duct.

As to the difference in size of the spermatogenic cysts present in the two types of treated animals, it is possible that the sudden arrival at a threshold level of hormone in the case of estradiol was responsible for a rapid differentiation of the gland, causing the smaller size of the spermatogenic elements. The pregneninolone-treated animals, which received a longer and steadier stimulation, were capable of producing cysts which were larger than those normally seen (see Text-fig. 3).

In order to suggest an explanation for the above effects and the others found in the present work, several assumptions must be made. First, it is well known that the liver of mammals inactivates steroid hormones which pass through the portal circulation (Biskind and Mark, 1939; Burrill and Greene, 1942; Cantarow *et al.*, 1943; Heller, 1940; Israel *et al.*, 1937; Segaloff, 1943; Talbot, 1939; Teague, 1941; Westerfeld, 1940). It is assumed that the same action takes place in the liver of teleosts. Some hormones, however, are inactivated more than others. Estradiol is inactivated more than estradiol benzoate because the benzoate ester protects the molecule from destruction. According to Heller (1940), the oxidation of the estradiols takes place at carbon 3 in ring A. Since the benzoate radical is attached at this position, its presence protects the molecule from oxidation (Segaloff, 1943). Therefore it can be assumed that the effective dose of estradiol, that is, the dose which produces the effects in the animal, is less than the effective dose of

estradiol benzoate, if identical oral doses are given.

The toxicity of the hormones must also be taken into consideration. Plate V, Fig. 23, shows the appearance of the typical liver of an animal treated with pregneninolone. The cells are greatly enlarged and vacuolated and are presumably in a condition caused by the relatively great toxicity of the pregneninolone, which may be interpreted as a type of fatty change. Because of this toxicity, the liver, which at first probably rapidly inactivated the hormone, was rendered unable to do so, and the main portion of the hormone passed through the liver intact, producing a large effective dose and intense effects. The estradiol, which is partially inactivated, causes also a partial vacuolization of the liver, suggesting a cumulative effect on the liver, which results in an increase in effective dose. This eventually has an effect on the gonads.

If these hypotheses are true, they present new evidence for the action of abnormal quantities of metabolic substances on the liver, since till now the only concusive evidence for the inhibition of inactivation by the liver has been derived from work on experimental Vitamin B deficiency (Biskind and Biskind, 1941, 1942, 1943; Biskind, 1946).

A further assumption concerns the stage of growth and differentiation in which the gonads are found during the period of the experiment. During this period the testes are, for the purposes of this explanation, in a relatively undifferentiated state and not yet under the influence of the pituitary. Gonadotrophic hormones are known to be present in fishes (Scheer, 1948). There is evidence to support the above assumptions. The testes, as shown by Text-fig. 2, grow very little during the period of the experiment. They contain essentially the same elements at the end of eight weeks as they possessed about one week after birth. The ovaries, on the other hand, grow considerably during the same period, and yolk deposition is begun and progresses considerably. The ovaries and eggs are much larger at the end of the period than they were at one week of age. The growth of the gonads is known to be under the control of the pituitary (Matthews, 1939a).

If these assumptions are admitted, at least as possibilities, a hypothesis may be advanced as to the method by which the hormones produce their results in these experiments.

In the case of the testis, the first effective doses of pregneninolone were small because the substances were largely inactivated by the liver tissue. These relatively small doses stimulated the pituitary rather than inhibited it because of the smallness of the dose. The estradiol had a delayed effect because it continued to be inactivated for a longer period of time, and therefore needed a longer period of time in which to reach an effective dose. The dose which was effective in the case of estradiol was a cumulative one and required a longer period in which to operate and a larger animal on which to operate because of some type of threshold reaction. The estradiol benzoate went through the liver tistue undestroyed and reached the pituitary in doses large enough to cause an inhibition rather than a stimulatory effect. Thus the testis, which was not yet under pituitary control, showed little effect from the administration of this drug.

In the case of the ovaries, which were already under pituitary control, the effects were different. The smaller doses of estradiol and pregneninolone acted as partial inhibitors, shown by the partial inhibition of the eggs in these specimens, while the estradiol benzoate, again passing through the liver undestroyed, caused an almost complete inhibition of growth of the eggs.

To suggest an explanation for the action on the gonopodium is a more difficult problem. In both males and females, the effect on the gonopodium was similar. Pregneninolone stimulated at least some growth in all gonopodia, and all older animals treated for a longer period of time showed almost perfect transformation of the fin. Estradiol stimulated all gonopodia to a slight growth, and the largest ones to the same type of differentiation shown by the pregneninolone animals, though the differentiation was slightly less advanced. Estradiol benzoate had no effect on any of the animals. There are a number of hypotheses which may be advanced.

First, the gonopodium might be under purely genetic control. It is known that this is not true because the treated females showed differentiation to a gonopodium as readily as did the males.

Second, the ovarian hormone might inhibit the gonopodium. If we can assume that an inhibited ovary is producing little or no hormone, the above hypothesis cannot be true because under these conditions a greatly inhibited ovary would allow a better differentiated gonopodium than a partially inhibited one. The estradiol benzoate-treated ovary was inhibited to the greatest degree, but there was no gonopodium, while the animals which possessed partially inhibited ovaries formed well differentiated gonopodia.

Third, the reactions cannot be due to a non-specific reaction to steroids because the different substances produced different effects.

Fourth, if the reactions are due to the action of the fish testis hormone, or to an androgenic effect directly, it must be hypothesized that estradiol has a direct androgenic effect, while an effect based on dosage difference would be more plausible, since in mammals the substance has an estrogenic effect.

Fifth, control from the pituitary gland entirely could explain the effects in the males, where pregneninolone and estradiol stimulate the pituitary. In the females, however, the pituitary, according to the above assumptions, and based on its action on the gonads,

inhibits the ovaries, and presumably would not at the same time stimulate the differentiation of a gonopodium. This of course assumes that the gonadotrophins secreted by both male and female pituitaries are qualitatively identical and stimulate the gonads of the animals in which they exist. This has been shown to be true for amphibians (Rugh, 1935).

Sixth, the theory that pituitary control plus male gonads or androgenic hormone cause the effects is the most nearly complete explanation. In this case, pregneninolone and estradiol stimulate the pituitary and therefore stimulate the gonopodium through the gonad. Estradiol benzoate inhibits the pituitary. Since the testis is not as yet under pituitary control, the testis shows no effects. No androgenic hormones are produced and the lack of these produces, in turn, lack of a gonopodium. In the females, however, an androgenic effect of the substances administered is necessary to explain the results. Pregneninolone and estradiol inhibit the pituitary and through it inhibit the ovary. The pituitary inhibition plus the androgenic effects of the hormones cause the differentiation of the gonopodium. Estradiol benzoate inhibits the pituitary, but, having no androgenic effect, does not cause the formation of the gonopodium.

A detailed cellular examination of the pituitary gland in these fish may reveal significant differences between controls and experimental animals, presumably involving the cells which secrete gonadotrophic hormones. This may furnish a partial explanation for the results described above and indicate whether the action may take place through the pituitary or is a direct effect of the hormones upon the gonads, as has been shown to happen in other animals (Nelson, 1937). A careful examination of the interstitial tissue of the testes may also aid in determining the possible effects of the hormones upon this tissue.

These hypotheses were constructed in an attempt to correlate the actions of the various hormones on the gonads and on the anal fin. Perhaps the effects on the two are entirely separate, however. The effect of the pituitary may be brought in to account for the effects on the gonads, but an androgenic effect of estradiol and pregneninolone would account alone for the effects on the gonopodium. It cannot be assumed, however, in view of the evidence brought out by estradiol benzoate treatment, that the effect is the paradoxical estrogen effect mentioned above caused by high dosage with estrogens. The effective dose of estradiol benzoate is higher than that of the others because it is protected in the liver. Therefore, under these conditions, one would be led to expect that it would produce a more definite effect than either of the other hormones. Since this is not true, some other hypothesis must be advanced to explain this effect. The other possibility which is most plausible is one in which the hormone has a directly androgenic effect.

The fact that the hormones which were used produced uniform results in spite of more than a tenfold range in dosage is an unusual finding. The toxicity which was found to be present with large dosages has also been found in mammals, but no sub-maximal results were found here.

It might have been useful also to treat the fishes with other benzoates as a control for the possible action of the benzoate ester exclusive of estradiol. The use of an inactive free compound with an active benzoate ester would be helpful in this work.

Turner (1941 a and b) brought to light various factors affecting the growth of the gonopodium. He stated that, first, the growth of the gonopodium depended on a certain low concentration of hormone and the differentiation of the fin depended on a higher concentration; second, that there existed certain dominances in the ray complexes which governed the differential growth of the various rays in such a way as to produce what we know as a complete gonopodium if the fin is left undisturbed; and third, that castration at any time during the growth of the gonopodium would stop its growth, while the administration of androgens thereafter would renew its growth. These findings on *Gambusia* have important bearings on the present studies. It was suggested above that the effect of estradiol was a cumulative one. This might account, on the basis of Turner's first statement, for the anal fin growth shown by the smaller estradiol-treated animals, where no differentiation was present. Pregneninolone caused an immediate and sustained effect on the gonopodium, suggesting that this hormone reached the threshold level almost immediately. Such a hypothesis would aid in explaining the effects on both testes and gonopodia.

As to the effect on the females, the hormones, as suggested above, may have had a direct effect on the fins.

The differential growth of the 3, 4, 5 ray complex was apparently governed by a low concentration of hormone. Dominance then shifted, according to Turner, so that the rays outside the 3, 4, 5 complex were subordinated to these three. This might explain the rapid growth of these rays in the young estradiol males and others in which a low level of hormone existed.

Castration with the effect of termination of growth of the fin, followed by androgenic restimulation, shows that the testis itself is not necessary for the growth of the fin, but that a hormone similar to that produced by the testis is required. This might aid in explaining the cases in which the females grew well-formed gonopodia.

The above hypotheses are far from clear and more work must be done in order to determine the explanation for these seemingly opposite and confusing effects. Hypophysec-

tomy, castration and a combination of the two performed on animals which were later treated with hormones would aid in determining the mechanisms which govern these effects. Preparations for such work are going on now.

More work is necessary on the general problem of the differential effects of these two estradiol compounds. The exact stage when the differential effect on the male begins should be studied in more detail. Smaller dosages should be used in an attempt to discover a dose small enough to secure a less than maximum effect, as such an effect does not appear in the present work. Finally, an investigation into the differential effects of more compounds related to these should be carried out, since the exact effect of any one of them is now doubtful, whereas heretofore they have been used interchangeably, at least on experimental animals.

## Summary.

1. The experimental animal used was a strain of the platyfish in which males could be distinguished from females at birth as a result of a Y chromosome sex linked, spotted factor, whereas usually the sexes are indistinguishable until maturity, when the anal fin of the male is transformed into an intromittent gonopodium.

2. The hormones used were alpha estradiol, alpha estradiol benzoate and pregneninolone, a synthetic progestogen. These were administered by mixing the powder or oil solution with the food.

3. Pregneninolone exhibited a strong stimulating effect on the males, with precocious maturation of the testes and well-formed gonopodia. In females, development of the ovaries was inhibited, and gonopodia produced.

4. Estradiol benzoate was inhibitory on the testis and greatly so on the ovary. No gonopodia were produced.

5. Alpha estradiol had no effect on the testes of males under 18 mm. in standard length and produced slight growth of the anal fin. In males over 19 mm. in length, the testes were greatly stimulated and large, well-formed gonopodia were found. All females so treated showed ovarian degeneration and partial to nearly complete gonopodia.

6. Studies on the liver showed that pregneninolone and estradiol produced great vacuolization of the parenchyma cells and resulted in an organ which showed fatty changes, while the benzoate-treated livers appeared like those of the controls.

7. It is to be emphasized that although in the amniotes, estradiol and its ester are used interchangeably, in this species the two compounds produce diametrically opposed effects under the conditions of these experiments.

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## EXPLANATION OF THE PLATES.

### Plate I.

Fig. 1. Testis of control male eight weeks of age. ×100.

Fig. 2. Testis of estradiol benzoate-treated male eight weeks of age. ×100.

Fig. 3. Testis of pregneninolone-treated male eight weeks of age. ×100.

Fig. 4. Testis of estradiol-treated male eight weeks of age. ×100. Compare with Fig. 3.

Fig. 5. Testis of estradiol-treated male eight weeks of age. ×100. Compare with Figs. 3 and 4.

### Plate II.

Fig. 6. Ovary of control female eight weeks of age. ×100.

Fig. 7. Ovary of estradiol benzoate-treated female eight weeks of age. ×100.

Fig. 8. Ovary of pregneninolone-treated female eight weeks of age. ×100.

Fig. 9. Ovary of pregneninolone-treated female eight weeks of age. ×100. Note scattering.

Fig. 10. Ovary of pregneninolone-treated female eight weeks of age. ×100. Note bilobed appearance of organ.

Fig. 11. Ovary of estradiol-treated female eight weeks of age. ×100. Compare with Fig. 9.

### Plate III.

Fig. 12. Ovary of estradiol-treated female eight weeks of age. ×100. Note large degenerating eggs and small abnormal eggs.

Fig. 13. Anal fin of control male. ×34.

Fig. 14. Anal fin of estradiol benzoate-treated male. ×34. Compare with Fig. 13.

Fig. 15. Anal fin of pregneninolone-treated male. ×34. Note almost complete differentiation of gonopodium. Compare with Fig. 13.

Fig. 16. Anal fin of estradiol-treated male. ×34. Compare with Figs. 13 and 15.

### Plate IV.

Fig. 17. Anal fin of control female. ×34.

Fig. 18. Anal fin of estradiol benzoate-treated female. ×34. Compare with Fig.17.

Fig. 19. Anal fin of pregneninolone-treated female. ×34. Compare with Figs. 15 and 17.

Fig. 20. Anal fin of estradiol-treated female. ×34. Compare with Figs. 16, 17 and 19.

### Plate V.

Fig. 21. Liver of control animal. ×960.

Fig. 22. Liver of estradiol benzoate-treated animal. ×960. Note similarity to Fig. 21.

Fig. 23. Liver of pregneninolone-treated animal. ×960. Note extensive vacuolization. Compare with Fig. 21.

Fig. 24. Liver of estradiol-treated animal. ×960. Note vacuolization—approaching but not equalling that of Fig. 23.

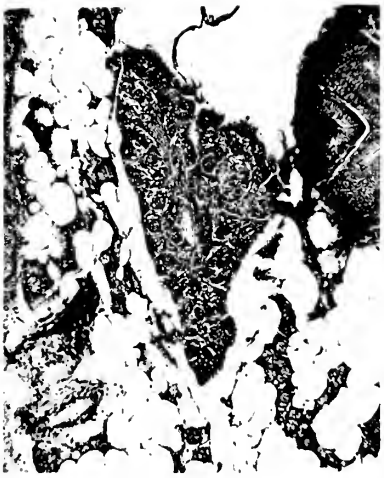

FIG. 1.

FIG. 2.

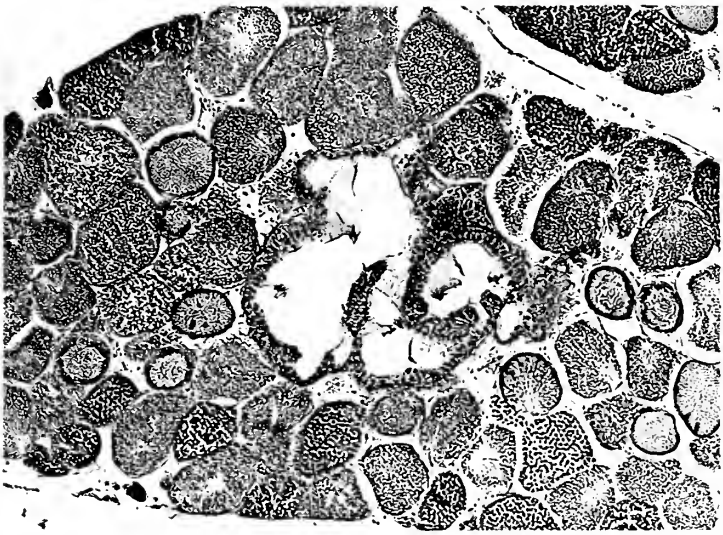

FIG. 3.

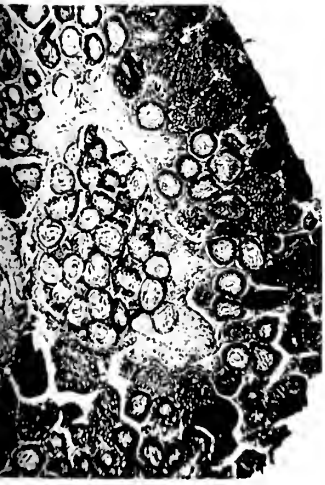

FIG. 4.

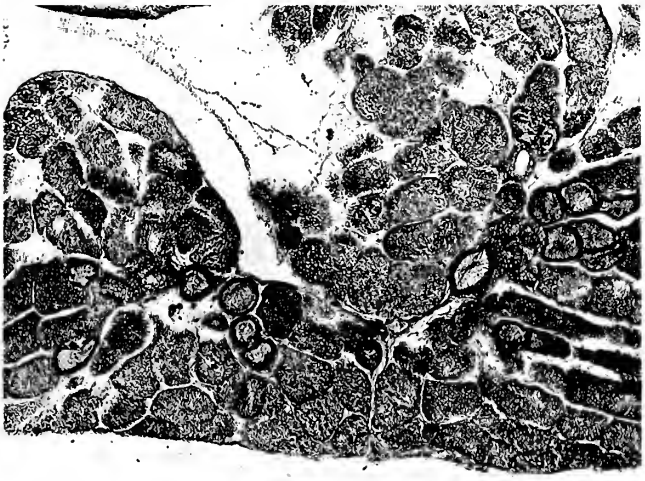

FIG. 5.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.

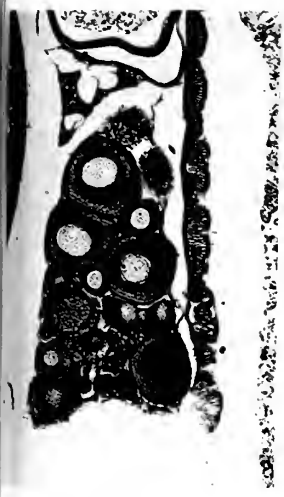

FIG. 6.

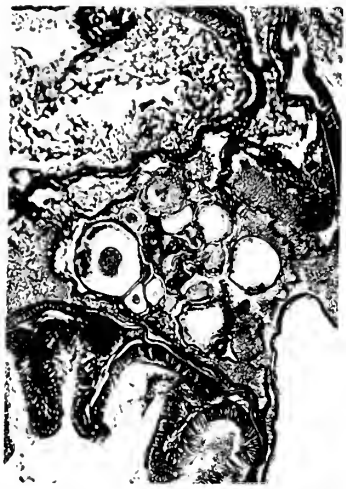

FIG. 7.

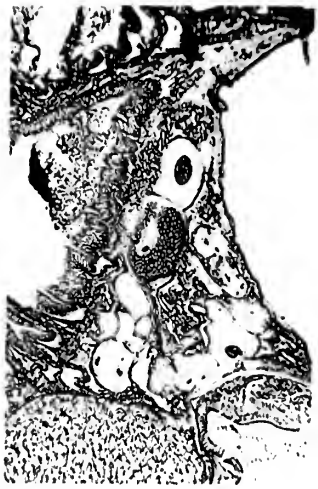

FIG. 8.

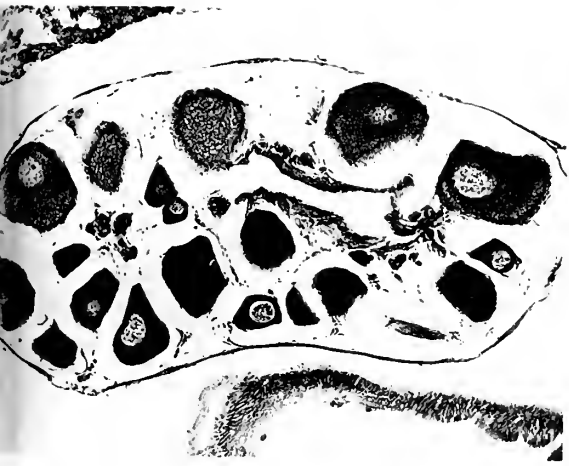

FIG. 9.

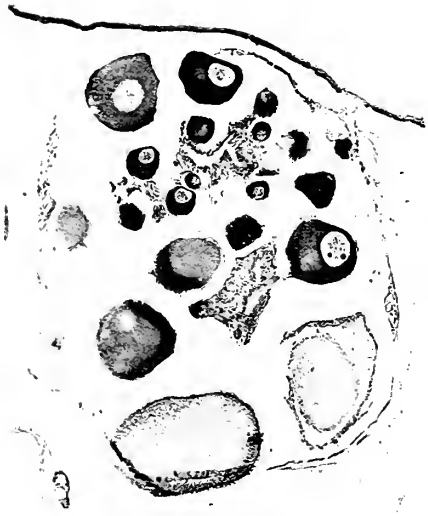

FIG. 11.

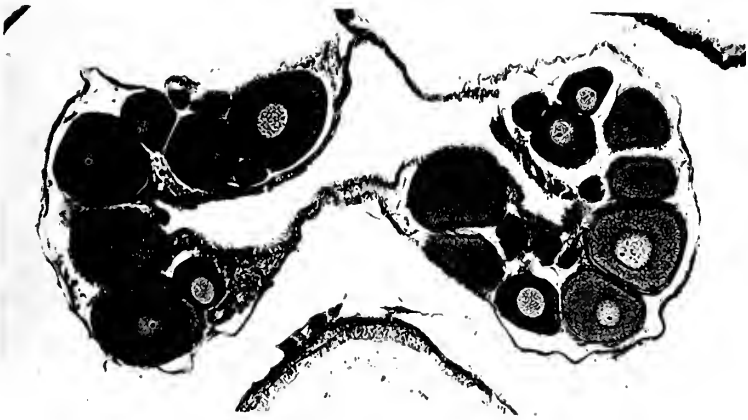

FIG. 10.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.

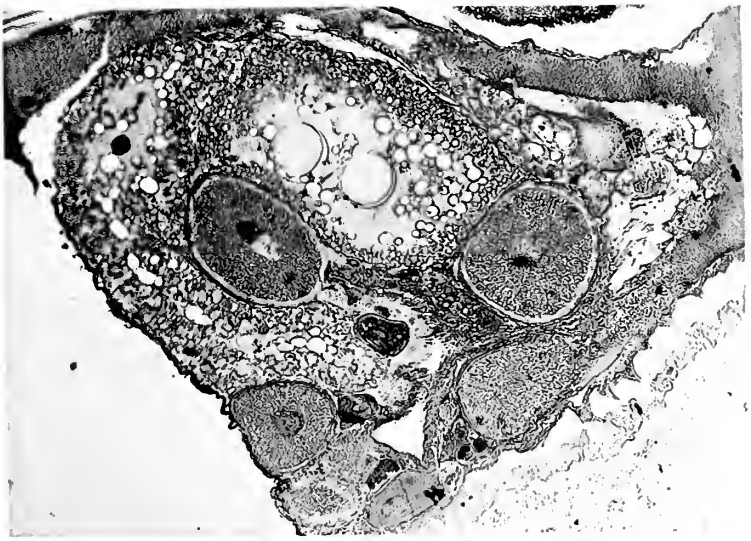

FIG. 12.

FIG. 13.

FIG. 14.

FIG. 15.

FIG. 16.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.

FIG. 17.

FIG. 18.

FIG. 19.

FIG. 20.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.

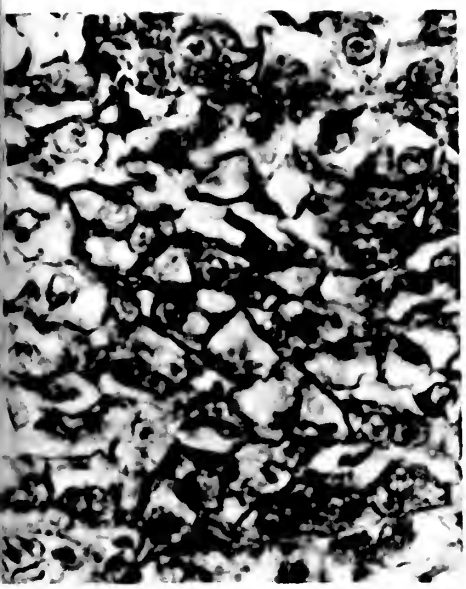

FIG. 21.

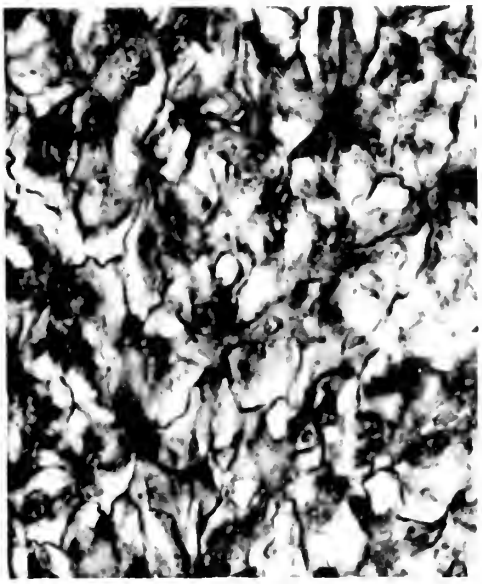

FIG. 22.

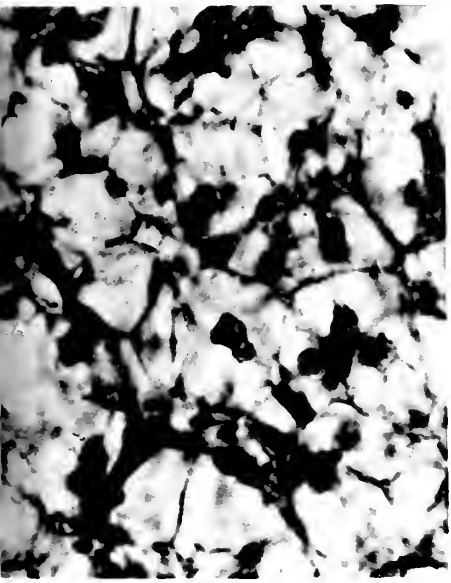

FIG. 23.

FIG. 24.

DIFFERENTIAL EFFECTS OF ESTRADIOL, ESTRADIOL BENZOATE AND PREGNENINOLONE ON PLATYPOECILUS MACULATUS.

# 19.

## Eastern Pacific Expeditions of the New York Zoological Society. XLI. Mollusks from the West Coast of Mexico and Central America. Part VIII.[1]

LEO GEORGE HERTLEIN & A. M. STRONG.
*California Academy of Sciences.*

(Plate I).

[This is the forty-first of a series of papers dealing with the collections of the Eastern Pacific Expeditions of the New York Zoological Society made under the direction of William Beebe. The present paper is concerned with specimens taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). For data on localities, dates, dredges, etc., refer to *Zoologica*, Vol. XXII, No. 2, pp. 33-46, and Vol. XXIII, No. 14, pp. 287-298.]

CONTENTS.



### INTRODUCTION

This is the eighth of a series of papers dealing with collections of mollusks taken on the Templeton Crocker Expedition (1936) and the Eastern Pacific *Zaca* Expedition (1937-1938). The general plan of presentation followed in the present contribution is that mentioned in Part II of this series of papers[2]. Formal headings and keys are given for the species collected by the expeditions of 1936 and 1937-1938. Occasionally additional species are included in the keys for convenience but in such cases it is indicated which species do not occur in the present collection.

Acknowledgment is due Dr. G. D. Hanna, Curator, Department of Paleontology of the California Academy of Sciences, Mr. A. G. Smith, Research Associate of the same institution, and Dr. A. Myra Keen, Stanford University, California, for assistance and suggestions. The photographs used for illustrations on the plate were prepared by Mr. Frank L. Rogers.

### FAMILY SEMELIDAE.

A paper by Dall[3] dealing with the west American Semelidae and one by Lamy[4] which contains a revision of the species of this group in the Natural History Museum in Paris are useful to anyone studying the Recent west American forms of this family.

KEY TO THE GENERA OF THE SEMELIDAE.

A. Pallial sinus free from the pallial line ..... *Semele*

B. Pallial sinus confluent with the pallial line

  a. Length exceeding 10 mm.; moderately thick ..... *Cumingia*

  aa. Length rarely exceeding 10 mm.; very thin; usually smooth ..... *Abra*

### Genus *Semele* Schumacher.

KEY TO THE SPECIES OF *Semele*.

A. Concentrically sculptured with coarsely corrugated or wrinkle-ribbed ridges

  a. Exterior with radial striae or wrinkled and granulated sculpture

    b. Interior white; dorsal margin purple; truncated posteriorly ..... *decisa*

[1] Contribution No. 859, Department of Tropical Research, New York Zoological Society.

[2] Hertlein, L. G., and Strong, A. M. Eastern Pacific Expeditions of the New York Zoological Society. XXIII. Mollusks from the West Coast of Mexico and Central America. Part II. *Zoologica*, New York Zool. Soc., Vol. 28, Pt. 3, December 6, 1943, pp. 149-168, 1 pl. See especially pp. 149-150.

[3] Dall, W. H. Notes on the Semelidae of the West Coast of America, including some new species. *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, issued March 2, 1915, pp. 25-28.

[4] Lamy, E. Révision des Scrobiculariidae vivants du Muséum d'Histoire Naturelle de Paris. *Journ. de Conchyl.*, Vol. 61, No. 3, March 25, 1914, p. 243-368, pl. 8, also figs. in text.

bb. Interior brown, orange or yellow
c. Interior brown; corrugated *tabogensis*
cc. Interior yellow or orange; wrinkle-ribbed exteriorly *californica*
aa. Exterior without radial sculpture *craneana*
B. Concentrically sculptured with raised threads, lamellae, or growth lines only
a. Concentric sculpture of growth lines only
b. Diagonal striae present *sparsilineata*
bb. Diagonal striae absent; smooth, pure white ..... *laevis*
aa. Concentric sculpture of raised threads or lamellae
c. Escutcheon wide, strongly beveled ..... *flavescens*
cc. Escutcheon very narrow or lacking
d. Shell without radial sculpture; white
e. Interspaces with fine concentric striae *paziana*[5]
ee. Interspaces without fine concentric striae *simplicissima*
dd. Shell with radial sculpture
f. Shell with incised radial grooves on part or all of valves
g. Incised sculpture along anterior dorsal margin only
h. Concentric ribs closely spaced, fine
i. Shell thick, fairly high; interior with a deep purple blotch ..*pulchra*
ii. Shell thinner, more elongate; less purple coloration *quentinensis*
hh. Concentric ribs more widely spaced, coarse *guaymasensis*
gg. Incised sculpture present along anterior and posterior margins
j. Concentric ribbing fine *jaramija*
jj. Concentric ribbing coarse; entire valve often reticulately sculptured ..*pacifica*
ff. Shell without incised radial grooves; fine radial striae present, stronger in interspaces
k. Shell suborbicular or roundly ovate
l. brownish - red with white medial streak on umbos; large *jovis*
ll. Yellowish or white *mediamericana*[5]
kk. Shell elongate
m. Concentric lamellae high; shell large; white with purple spots
n. Lamellae with scalloped scale-like projections *verrucosa*
nn. Lamellae without scale-like projections; more rounded ventrally *formosa*[5]
mm. Concentric lamellae low; shell small; umbos purplish or brownish
o. Thick; end of pallial sinus slightly attenuated *venusta*
oo. Thin; end of pallial sinus blunt *incongrua*[5]

**Semele corrugata californica** Reeve.

*Amphidesma californica* Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 19, pl. 3, fig. 19. "Gulf of California."

[5] Not represented in the present collection.

*Semele californica* A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 96. "Hab. Gulf of California. Mus. Cuming."

*Type Locality:* Gulf of California.

*Range*: Magdalena Bay, Lower California, to the Gulf of California.

*Collecting Station:* Mexico: Cape San Lucas, Lower California, beach.

*Description:* Shell ovately oblong, subequilateral, dirty pale brown, radiately striated; transversely sulcated, ribs elevated, subcorrugated, ornamented, interspaces closely longitudinally striated; anterior side rounded, posterior subtruncated, very flexuous; interior yellowish, margin yellow. (Free translation of Adams' original description.)

The shell of this subspecies is characterized by the concentric wrinkle-ridged ribs and the dense minute radial striae. A small lunule is present but no appreciable escutcheon. Exteriorly the shells are usually yellowish or yellowish-white in color. The umbos are often yellow and on some specimens a few faint brown transverse markings are present on the dorsal margin both anterior to and posterior to the beaks. Interiorly the shells are usually yellow, sometimes a beautiful golden or orange-yellow. The pallial sinus ascends gently and is rounded at the end which extends forward a little over one-half the length of the shell.

A left valve from Cape San Lucas, in the present collection, measures: length, 40.2 mm.; height, 36 mm.; convexity (one valve), 7.3 mm. A specimen from Magdalena Bay, Lower California, in the Henry Hemphill Collection of the California Academy of Sciences measures: length, 37.5 mm.; height, 33.6 mm.; convexity (both valves together), 15.2 mm.; pallial sinus extends anteriorly 22 mm. from the posterior margin of the shell.

This form apparently is, as stated by Dall, closely related to *Semele corrugata* Sowerby[6]. The specimens which we have seen from Magdalena Bay and the Gulf of California appear to be a little smaller than those of *S. corrugata* Sowerby which was described from Peru. Furthermore these do not have the purple coloration on the anterior portion of the hinge as shown on Reeve's illustration of *Semele corrugata*. That species has been recorded as occurring at Magdalena Bay and in the Gulf of California, and it is possible that the present specimen might be referable to Sowerby's species. However, for the present at least, we are inclined to regard these northern shells as belonging to a subspecies of *S. corrugata*, at least until a comparison can be made with a series of specimens from Peru, the type locality of Sowerby's species.

It appears that in some cases, *Semele corrugata californica* has been confused with *Semele flavescens* Gould, a different shell.

*Distribution:* A single valve of this subspecies was taken by the expedition on the beach at Cape San Lucas. It also occurs in the Pleistocene of Magdalena Bay, Lower California. The record "*Semele* cf. *pulchra* Sowerby" in the list of species cited by Jordan, 1936, as occurring in the Pleistocene of Magdalena Bay, is referable to *S. corrugata californica*. Olsson has recorded "*Semele* cf. *californica* Con." as occurring in the Pleistocene of Panama. Records of the occurrence of this shell in Asiatic seas are referable to some other species.

**Semele craneana** Hertlein & Strong, sp. nov.

Plate I, Figs. 19, 22.

Shell oval, compressed, thin, with the beaks a little nearer the posterior end, yellowish, with faint, pinkish, interrupted radial stripes; posterior dorsal margin sloping, slightly convex, forming a distinct angle with the truncated posterior end, anterior dorsal margin more direct, slightly concave, anterior dorsal margin well rounded; lunule very small, indistinct; outer surface smooth near the beaks gradually developing concentric ridges which are strongest near the margins, with deep interspaces which about equal the ridges in width; posterior end with a depression running from near the beaks to the lower end of the truncation, posterior to which the shell is flattened and somewhat flexed; radial sculpture entirely absent; interior white, somewhat iridescent, showing the concentric sculpture and pinkish rays quite distinctly; pallial sinus broad, ascending, rounded at the end and projecting about two-thirds the length of the shell; two cardinal teeth, the posterior one the larger, lateral teeth small. The type measures: length, 38 mm.; height, 29.5 mm.; convexity (one valve), 6.5 mm.; pallial sinus projects forward 24 mm. from the posterior margin of the shell.

Holotype, a left valve, (Calif. Acad. Sci. Paleo. Type Coll.), dredged in the Gulf of California. One left valve was dredged on Arena Bank, Gulf of California, Station 136-D-24, Lat. 23°29′ N., Long. 109°23′30″ W., in 50 fathoms (91 meters), mud, *Arca* conglomerate; one young specimen and a single right valve were dredged in the same general locality, Station 136-D-26, Lat. 23°27′ N., Long.

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[6] *Amphidesma corrugatum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, species No. 8, issued between January 18 and March 8, 1833. [Not illustrated]. "Iquiqui, Peru. Mr. Cuming." Ref. to "Spec. Conch. f. 18." [The exact dates of issue of the Species Conchyliorum is unknown to us. A copy of Volume 1, Part 2, in the library of the California Academy of Sciences is not dated. In Hanley's edition of Wood's Index Testaceologicus, 1856, p. XIX, the dates cited for Sowerby Species Conchyliorum are, "part 1. 1830: part II. (imperfect) not published until Nov. 1855"]. —Sowerby, *Proc. Zool. Soc. London* for 1832, issued March 13, 1833, p. 200. "Hab. in Peruviâ et ad Iquiqui." "Dredged from coarse gravel in ten fathoms water."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 4, pl. 1, fig. 4 (as *Amphidesma corrugata*). [Locality same as in preceding reference].

Shaw (*Proc. Malacol. Soc. London*, Vol. 8, No. 6, 1909, pp. 333-340), in a collation of the Conchological Illustrations, indicated that Parts 17, 18, 19, and the catalogue of species of *Amphidesma* issued with Part 19, appeared between January 18 and March 8, 1833. The species of *Amphidesma* named and illustrated in those parts for the first time take their date of publication from the Conchological Illustrations rather than the *Proceedings* of the Zoological Society of London where the descriptions appeared on March 13, 1833.

109°24′ W., in 45 fathoms (82 meters), sand, crushed shell; a single valve was dredged 3 miles off Pyramid Rock, Clarion Island, Station 163-D-2, Lat. 114°45′ N., Long. 114° 45′ W., in 55 fathoms (100 meters), rock, coral.

This shell is similar in size and shape to *Semele tabogensis* Pilsbry & Lowe. The sculpture is similar but lacks the fine radial ornamentation of that species and the posterior area is more distinct.

The shell of *Semele craneana*, although less arcuate ventrally, is similar to that of *S. martinii* Reeve[7] which was originally described from Brazil.

This species is named for Miss Jocelyn Crane, Technical Associate, Department of Tropical Research, New York Zoological Society, who accompanied the Templeton Crocker Expedition, 1936, during the course of which the type specimen of the present species was collected.

*Distribution:* This new species is at present known only from the southern portion of the Gulf of California and from off Clarion Island, in 45-55 fathoms.

### **Semele decisa** Conrad.

*Amphidesma decisa* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 239, pl. 19, fig. 2. "Inhabits with the preceding" [which is "Inhabits deep water in the vicinity of Sta. Diego".]—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 24, pl. 4, fig. 24. San Diego, California.

*Semele decisa* Conrad, Grant & Gale, *Mem. San Diego Soc. Nat. Hist.*, Vol. 1, 1931, p. 376, pl. 14, figs. 13a, 13b. Earlier records cited. Pleistocene and Recent.

*Type Locality:* San Diego, California, in deep water.

*Range:* San Pedro, California, to Cape San Lucas, Lower California.

*Collecting Station:* Mexico: Cape San Lucas, Lower California.

*Description:* Shell rounded, thick, subequilateral, the anterior side the longer, the end rounded; posterior dorsal margin nearly straight, the posterior end truncated; posteriorly biangulate, the area between somewhat concave; ornamented with numerous, thick, unequal concentric rugose ribs, the entire surface covered with fine radial grooves or fine wrinkled and granulated sculpture; colored exteriorly by whitish-gray with occasional purple in the concentric grooves; cardinal teeth obsolete, laterals present; pallial sinus wide, rounded at the end, slightly ascending and extending forward about five-eighths the length of the shell which is past a line vertical with the beaks; interior white with purple around the dorsal margin.

A specimen from Cape San Lucas, Lower California, measures: length, 45 mm.; height, 42.5 mm.; convexity (both valves together), 19.8 mm.; pallial sinus extends anteriorly 27 mm. from the posterior margin of the shell. A large specimen of this species from Magdalena Bay, Lower California, in the Henry Hemphill collection of the California Academy of Sciences measures: length, 94 mm.; height, 86.5 mm.; convexity (both valves together), 45.5 mm.; pallial sinus extends anteriorly 59 mm. from the posterior margin of the shell.

The shell of *Semele punctata* Sowerby[8], which was described from the Galápagos Islands, is more elongate in outline and less truncated posteriorly than that of *S. decisa*.

*Semele nisigotoensis* Nomura & Hatai[9], described from the Miocene of Japan, was compared to *S. decisa*.

*Distribution:* A few specimens of this species were collected by the expedition at Cape San Lucas, Lower California. This is an extension south of the known range of the species. It also has been recorded as occurring in the Pleistocene of Tomales Bay in Central California, in southern California, and south to Magdalena Bay, Lower California.

### **Semele flavescens** Gould.

*Amphidesma flavescens* Gould, *Proc. Boston Soc. Nat. Hist.*, Vol. 4, November, 1851, p. 89. "San Diego, Lieut. Green."—Gould, *Boston Jour. Nat. Hist.*, Vol. 6, 1853, p. 392. Original locality cited.

*Amphidesma proximum* C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, pp. 513, 547 (separate, pp. 289, 323). "Habitat. — Panama." — Hanley, Cat. Rec. Bivalve Shells, p. 341, 1856, pl. 12, fig. 5, 1843 (cited as *Amphidesma corrugatum* on expl. to plate). "Mexico."

*Amphidesma proxima* Adams, Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 20, pl. 3, fig. 20. "Hab. Panama." [A reproduction of this figure given by M. Smith, Panamic Mar. Shells (Tropical Photogr. Lab., Winter Park, Florida), 1944, fig. 805].

*Semele flavescens* Gould, Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 358. Gulf of California; Panama.

*Semele proxima* C. B. Adams, Olsson, *Nautilus*, Vol. 37, No. 4, 1924, p. 129. Zorritos, Lobitos, Negritos, Peru.

*Type Locality:* San Diego, California.

*Range*: Catalina Island, California (Dall), to Negritos, Peru.

*Collecting Station:* Costa Rica: Golfito Bay, Gulf of Dulce.

*Description*: Shell subrotund, compressed, sculptured by concentric lamellar decussate striae, orange becoming white in later stages and covered with a periostracum which is

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7 *Amphidesma martinii* Reeve, Conch. Icon., Vol. 8, *Amphidesma*, November, 1853, species 43, pl. 6, fig. 43. "Hab. Rio." [A. Adams' description of this species did not appear until July 25, 1854].

8 *Amphidesma punctatum* Sowerby, Conch. Illustr., *Amphidesma*, Catal. issued with Pt. 19, No. 18, pl. 18, fig. 7, issued between January 18 and March 8, 1833. "Galapagos Islands. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 200. "Hab ad Insulas Gallapagos."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 26, pl. 4, fig. 26 (as *Amphidesma punctata*). Galápagos Islands.

9 *Semele nisigotoensis* Nomura & Hatai, *Saito Ho-On Kai Mus. Res. Bull.*, No. 10, 1936, p. 131, pl. 16, figs. 8, 9. Nisigôto. Tanagura Beds, northwest Honsyu, Japan, middle Miocene.

brown shaded with gray (fusco); beaks median, acute, not at all elevated; anterior dorsal area excavated, posterior lanceolate, concave bounded by a line; interior tinted yellow, marked with shiny dots; pallial sinus spatulate, sculptured by close divergent striae; ligamental pit deep, elongate; anterior lateral teeth approximate to the beaks. Long. 2⅜; alt. 2⅛; lat. 1¼ poll. (Translation of Gould's original description).

"Usually found about half the above size; the concentric lamellae become worn off and more irregular towards the margin. The interior is faintly tinted yellow when young, but very richly so when old. It is near *A. corrugatum,* Sowb."

The description given by Gould in 1853 is an enlargement of the original. He stated: . . . "posterior dorsal edge long lanceolate, concave, bounded by a distinct angle; surface pale orange near the beaks, becoming dingy white at the older stages, and covered by a dirty greenish epidermis; marked by concentric lamellar striae, crossed by fine radiating striae, especially across the disk."

A left valve in the present collection measures: length, 47.5 mm.; height, 43.8 mm.; convexity (one valve), 11.2 mm. A specimen from Loreto, Lower California, in the collections of the California Academy of Sciences measures: length, 58.5 mm.; height, 55.4 mm.; convexity (both valves together), 28.3 mm.; pallial sinus extends forward 36 mm. from the posterior margin. A large single left valve from Magdalena Bay, Lower California, in the collection of the same institution measures: length, 64.4 mm.; height, 63.4 mm.; convexity (one valve), 15 mm.; pallial sinus extends anteriorly 40 mm. from the posterior margin of the shell.

Gould's type specimen has never been illustrated but the foregoing description applies exactly to specimens of a species in the collection of the California Academy of Sciences which were collected from Lower California to Panama. This species is identical with the one illustrated by Reeve under the name of *Amphidesma proxima* Adams. According to Dall[10] Adams' species is identical with *Semele flavescens. Amphidesma proximum* C. B. Adams was founded upon a specimen from Panama 1.8 inches in length. It was said to be closely related to *Semele elliptica* Sowerby and *S. lenticulare* Sowerby. Carpenter[11] regarded *S. proxima* as identical with *S. elliptica.* Whether or not *S. proxima* is identical with *S. flavescens* may be open to doubt but certainly Reeve's figure attributed to that species is referable to *S. flavescens.*

In some cases *Semele flavescens* has been identified under the name of *Semele striosa* C. B. Adams[12]. That species was based upon a single specimen from Panama .78 inch in length and it appears uncertain exactly how it differs from related forms. In the original description it is mentioned . . . "corselet and lunule not well defined." This does not agree with *S. flavescens* which has a well developed escutcheon.

*Semele mediamericana* Pilsbry & Lowe[13] differs from *S. flavescens* in lacking the strong escutcheon and in the sculpture in which . . . "there are narrow, thread-like concentric ridges, coarser and more raised than in *S. flavescens,* a little less than one mm. apart on the lower part of the valve, and a very minute, dense, even radial sculpture throughout, diverging at both ends, and seen under the lens to be totally unlike the radial striation of *S. flavescens.*"

*Distribution:* A single left valve of *Semele flavescens* was taken by the expedition at Golfito Bay in the Gulf of Dulce. It occurs fairly commonly from Magdalena Bay to the Gulf of California and south to Panama and apparently to Peru. We have not seen specimens from north of Magdalena Bay, but the type locality is San Diego, and Dall cited it as occurring north to Catalina Island. It also occurs in the Pliocene of the Gulf of California region and in the Pleistocene of Magdalena Bay, Lower California, and it has been recorded as occurring in the Quaternary of Ecuador. Olsson, 1932, cited "*Semele* cf. *flavescens* Gould" as occurring in the Miocene of Peru.

**Semele guaymasensis** Pilsbry & Lowe.

*Semele guaymasensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 84, May 21, 1932, p. 92, pl. 12, figs. 8 and 9. "Guaymas, 20 fathoms."—E. K. Jordan, *Contrib. Dept. Geol. Stanford Univ.,* Vol. 1, No. 4, 1936, p. 145. Magdalena Bay, Lower California, Pleistocene. Also Gulf of California, Recent.

*Type Locality:* Guaymas, Sonora, Mexico, in 20 fathoms.

*Range:* Punta Penasco, Sonora, Mexico, to La Paz, Lower California.

*Collecting Station:* Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand.

*Description:* The shell is light buff, faintly mottled or obscurely rayed with dull light purple, the dorsal borders dark purple. Shape irregularly oval, nearly equilateral, strongly compressed; dorsal margin slightly convex behind, straight in front of the beaks; ends rounded; ventral margin strongly convex. Sculpture of strong, concentric ridges generally a little wider than their intervals, a little lamellar at the border of the escutcheon, and on the anterior end cut by about seven radial grooves. Escutcheon very narrow, flattened, with weak growth lines only, purple. Lunule small, sunken, the dorsal area beyond it pur-

10 Dall, W. H., *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 67, 1915, p. 25.

11 Carpenter, P. P., *Proc. Zool. Soc. London,* 1863, p. 367. Reprint in *Smithson. Miscell. Coll.,* No. 252, 1872, p. 203.

12 *Amphidesma striosum* C. B. Adams, *Ann. Lyceum Nat. Hist. New York,* Vol. 5, July, 1852, pp. 515, 547 (separate pp. 291, 323). "Habitat.—Panama."

13 *Semele mediamericana* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 84, May 21, 1932, p. 92, pl. 12, figs. 1, 1a, 2 (as *Semele mediamericanum* on expl. to pl.). "Nicaragua (McNeil)."

ple and smooth except for lines of growth. The interior is stained with dull purple on a buff or white ground, with purple markings on the ventral border. The pallial sinus occupies about two-thirds of the length. Length, 16 mm.; height, 12.3 mm.; semidiam. (right valve), 2.6 mm. Length, 22 mm.; height 17 mm.; semidiam. (right valve) 4 mm. (Original description.)

This species differs from *Semele pulchra* Sowerby and *S. quentinensis* Dall in the much coarser and more widely spaced concentric sculpture.

*Semele anteriocosta* Vokes[14], described from the Miocene of Trinidad, is similar to *S. guaymasensis* in its general characters but the strength of the ribbing appears to be intermediate between that of this species and *S. quentinensis*.

*Distribution:* A few specimens referable to this species were dredged by the expedition in Santa Inez Bay, in the Gulf of California, in 4-13 fathoms, on a sandy bottom.

### **Semele jaramija** Pilsbry & Olsson.

Plate I, Fig. 12.

*Semele jaramija* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia,* Vol. 93, September 9, 1941, p. 70, pl. 17, fig. 5. "Canoa formation, Punta Blanca." Ecuador, Pliocene.

*Type Locality:* Canoa formation, Punta Blanca, Ecuador, Pliocene.

*Range:* Santa Inez Bay, Gulf of California.

*Collecting Station:* Mexico: Santa Inez Bay, Gulf of California (145), on shore.

*Description:* Shell small, suboval in form, with the beaks placed a little in back of the middle; but little convex; the sculpture consists of strong, regular, concentric threads, well developed over the whole shell and at the anterior-upper end, these concentric threads are cut by a series of small radial grooves; at the posterior end the grooves, about 8 in number, are crossed by the concentric threads, the sculpture being beautifully cancellated. Length, 21 mm.; height, 16 mm.; semidiameter, 3.5 mm. (Original description.)

A left valve of this species in the present collection measures: length, 16 mm.; height, 12.2 mm.; convexity (one valve), 2.9 mm.; pallial sinus extends anteriorly 9.5 mm. from the posterior margin of the shell.

The present specimen agrees exactly with the illustration of *Semele jaramija* given by Pilsbry & Olsson.

As mentioned in the discussion of *Semele pacifica*, that species always has radial sculpture on both the anterior and posterior dorsal areas. The variation in *S. pacifica* Dall is so great that it appears quite possible that the form here cited as *S. jaramija* may be merely a subspecies of it.

[14] *Semele anteriocosta* Vokes, *Amer. Mus. Novit.*, No. 988, May 16, 1938, p. 14, fig. 5. Upper Miocene of Springvale, Trinidad, British West Indies.

*Semele guaymasensis* Pilsbry & Lowe and *S. quentinensis* Dall have radial sculpture usually only on the anterior dorsal area and when present at all posteriorly it is much less strongly developed than that on *S. jaramija*.

*Distribution*: A single left valve here referred to *Semele jaramija* was taken by the expedition on shore at Santa Inez Bay in the Gulf of California. This species has also been recorded as occurring in the Pleistocene of Panama and in the Pliocene at Punta Blanca, Ecuador.

### **Semele jovis** Reeve.

*Amphidesma jovis* Reeve, Conch. Icon., Vol. 8, *Amphidesma*, November, 1853, species 34, pl. 5, fig. 34. "Hab.—?"

*Semele jovis* A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 94. "Hab. ? Mus. Cuming."

*Tellina barbarae* Boone, *Bull. Bingham Oceanogr. Coll.* Peabody Mus. Yale Univ., Vol. 2, Art. 5, December, 1928, p. 9, pl. 1 (upper figure). "Pearl Islands, depth 12 fathoms."

*Type Locality*: Port Parker, Costa Rica (here designated as type locality). No locality cited originally.

*Range*: Kino Bay, Sonora, Mexico, in the Gulf of California, to the Las Perlas Islands, Panama.

*Collecting Stations*: Mexico: Port Guatulco (195-D-2), 3 fathoms, sand; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: Port Parker (203-D-1-3), 12-15 fathoms, sandy mud, crushed shell, shelly sand, algae, shelly mud.

*Description*: Shell somewhat roundly ovate, somewhat ventricose, anterior side slightly the longer; posterior side with a flexure, the end truncated; ornamented with rather thin, close-set, concentric lamellae; the interspaces with fine concentric lineation; extremely fine radial wrinkling present on fresh specimens but clearly noticeable on worn specimens; color rose-fawn, beaks red with a medial white streak; hinge with two cardinals and laterals in each valve; pallial sinus broadly elliptically rounded, projecting forward about four-sevenths the length of the shell; interior rose and white.

A right valve from Port Guatulco, Mexico, measures: length, 54.5 mm.; height, 45 mm.; convexity (one valve), 10.3 mm.; pallial sinus extends anteriorly 32.5 mm. from the posterior margin of the shell. A specimen collected by H. N. Lowe at Kino Bay, Sonora, Mexico, in the Gulf of California, measures 59 mm. in length.

*Semele rosea* Sowerby[15], described from Peru, is more orbicular in outline than *S. jovis*.

[15] *Amphidesma roseum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, species No. 5, pl. 17, fig. 1, issued between January 18 and March 8, 1833. "Tumbez, Peru. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad littora Peruviae." "A single valve was found at Tumbez in Peru."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 17, pl. 3, fig. 17 (as *Amphidesma rosea*). Tumbez, Peru.

According to Verrill the lamellae are more closely spaced and the plication of *Semele jovis* is nearer the outer edge as compared to that of *S. junonia* Verrill[16] which was described from La Paz, Lower California. He mentioned the presence of radiating striae in the interspaces of *S. junonia*, a feature also present and especially noticeable on somewhat worn specimens of *S. jovis*. According to Lamy[17] *Semele junonia* is only a variety of *S. rosea*.

*Distribution*: A few single valves of *Semele jovis* were dredged by the expedition off western Mexico, Nicaragua, and Costa Rica.

### **Semele laevis** Sowerby.

*Amphidesma laeve* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, No. 22, pl. 18, fig. 6, issued between January 18 and March 8, 1833. "Xipixapi. W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Xipixapi, Columbiae Occidentalis." "A single specimen of this very delicate species was dredged from a depth of ten fathoms in sandy mud."

*Amphidesma laevis* Sowerby, Reeve, Conch. Icon., Vol. 8, *Amphidesma*, November, 1853, species 50, pl. 7, fig. 50. Original locality cited.

*Type Locality*: Xipixapi [Jipijapa], Ecuador, in 10 fathoms, sandy mud.

*Range*: Champerico, Guatemala, to Jipijapa, Ecuador.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-1-2), 14 fathoms, mud; El Salvador: La Libertad (198-D-1-2), 13-14 fathoms, mud; Costa Rica: Gulf of Dulce.

*Description*: Shell elongately ovate, inequilateral, the anterior side the longer, smooth, exterior and interior white; anterior dorsal margin nearly straight, sloping, anterior end tapering and rounded; ventral margin curved; posterior dorsal margin rounded and highest just back of the beaks, posterior end rounded; a broad, shallow, radial groove is present on the posterior area and where this meets the ventral margin there is sometimes a vague truncation; surface smooth except for concentric lines of growth and an occasional concentric groove and sometimes with fine submicroscopic radial striae; hinge of right valve with two small cardinals, the posterior one bifid, the anterior one thin, two laterals present, left valve with two cardinals, the anterior one bifid, the posterior one thin, also projections of the margin which fit into corresponding sockets in the right valve; pallial sinus somewhat elevated above then broadly tapering to a rounded point which projects forward about five-eighths the length of the shell.

A large right valve from off La Libertad, El Salvador, measures approximately: length, 68 mm.; height, 53 mm.; convexity (one valve), 13 mm.; pallial sinus extends anteriorly 48.4 mm. from the posterior margin of the shell.

*Semele laevis* var. *costaricensis* Olsson[18] has been described from the Miocene of Costa Rica and later was cited as also occurring in the Miocene of Peru.

*Semele pallida* Sowerby[19], described from Ecuador, bears a resemblance, in general features, to *S. laevis* but differs in that it is less elongate anteriorly, less rounded posteriorly, the beaks are more anteriorly situated and the coloration was described as pale purple-fulvous.

*Distribution*: Specimens of this species were dredged off Guatemala and El Salvador in 13-14 fathoms and were taken on the beach of the Gulf of Dulce. These occurrences extend the known range of the species considerably to the north as heretofore it has not been reported north of Panama. This species also has been recorded as occurring in the Pleistocene of Panama and in the Pliocene at Puerto Jama, Ecuador.

### **Semele pacifica** Dall.

Plate I, Fig. 11.

*Semele pacifica* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 61, March 2, 1915, p. 27. "Catalina Island, California, to Acapulco, Mexico, in 9 to 21 fathoms."—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 180, pl. 3, fig. 5. Original range cited.—J. Q. Burch, *Min. Conch. Club South. Calif.*, No. 43, January, 1945, p. 17. "Dr. A. M. Keen advises 'Type locality of *S. pacifica* is: U. S. B. F. Sta. 2022, off La Paz, in 21 fms.'"

*Type Locality*: Off La Paz, Lower California, in 21 fathoms (Keen).

*Range*: Catalina Island, California, to the Gulf of California and south to Taboga Island, Panama.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California (145-D-1, 3), 4-13 fathoms, sand, also on shore; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; Golfito, Gulf of Dulce.

*Description*: The shell of this species is very similar to that of *Semele cancellata* Sowerby[20] which occurs in Atlantic waters.

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[16] *Semele junonia* Verrill, *Amer. Jour. Sci.*, Ser. 2, Vol. 69, No. 146, March, 1870, p. 217. "Near La Paz,— Capt. J. Pedersen."

[17] Lamy, E., *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 357.

[18] *Semele laevis* Sowerby, var. *costaricensis* Olsson, *Bull. Amer. Paleo.*, Vol. 9, Bull. 39, Pt. 2, June 21, 1922, p. 430 (258), pl. 32 (29), fig. 1. "Gatun Stage: Hill No. 3, Banana River." Costa Rica, Miocene.

[19] *Amphidesma pallidum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, sp. No. 3, pl. 17, fig. 3, issued between January 18 and March 8, 1833. "Salango, W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Salango, Columbiae Occidentalis." "Dredged in sandy mud at a depth of seven fathoms."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 22, pl. 4, fig. 22 (as *Amphidesma pallida*). Original locality cited.

[20] *Amphidesma cancellatum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, species No. 13, issued between January 18 and March 8, 1833. "Antigua and St. Vincents." Ref. to "Spec. Conch. f. 8."—Reeve, Conch. Icon., Vol. 8, *Aphidesma*, 1853, species 44, pl. 7, fig. 44 (as *Amphidesma cancellata*). "Hab.—?."

Dall stated in the original description that it . . . "differs from that Atlantic species in its smaller lunule, shorter and weaker right lateral tooth, and sharper and more delicate concentric sculpture."

A left valve in the present collection from Golfito, Gulf of Dulce, Costa Rica, measures: length, 20 mm.; height, 16.6 mm.; convexity (one valve), 4.6 mm.

*Semele pacific* is a very variable species. Young specimens have rather flattened shells and strong cancellate sculpture with the concentric lamellae well developed. In the adult stage the shells become thicker, more ventricose, and with the radial element in the sculpture as strong or stronger than the concentric. The radial sculpture is always present near the anterior and posterior dorsal margins and sometimes covers the whole shell.

*Semele pacifica* is one of a group of related species which vary in details of sculpture. *Semele venusta* Reeve has no radiating sculpture. *Semele guaymasensis* Pilsbry & Lowe has strong concentric sculpture but with incised radiating sculpture only on the anterior dorsal area. *Semele quentinensis* Dall has very fine concentric sculpture with radial sculpture on the anterior dorsal portion and, rarely, with a few faint striae along the posterior dorsal margin. *Semele pulchra* Sowerby has concentric and radial sculpture similar to that of *S. quentinensis* but the shell is higher in proportion to the length as compared to Dall's species. *Semele jaramija* Pilsbry & Olsson, described from the Pliocene of Ecuador, has concentric sculpture intermediate in strength between that of *S. quentinensis* and *S. guaymasensis*, but in addition to similar radial sculpture on the anterior dorsal area it also has strong, incised radial sculpture on the posterior dorsal area. *Semele pacifica* has strong well developed concentric sculpture with radials on both the anterior and posterior portions and sometimes all over the shell.

*Distribution*: A few specimens of *Semele pacifica* were dredged by the expedition in 4-13 fathoms in Santa Inez Bay, in the Gulf of California, at Port Parker, Costa Rica, in 12 fathoms, and at Golfito in the Gulf of Dulce.

### ***Semele pulchra*** Sowerby.

Plate I, Fig. 15.

*Amphidesma pulchrum* Sowerby, *Proc. Zool. Soc. London*, June 5, 1832, p. 57. "Hab. in Sinu Caraccensi, Americae Meridionalis." —Sowerby, Conchyl. Illustr., Catal. issued with Pt. 19, species No. 2, pl. 17, fig. 2, issued between January 18 and March 8, 1833, "St. Elena W. Columbia." Var. fig. 2*. Panama.

*Amphidesma pulchra* Sowerby, Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 2, pl. 1, fig. 2. Original locality cited.

*Type Locality*: Bay of Caraccas, Ecuador.

*Range*: Gulf of Fonseca, Nicaragua, to Ecuador.

*Collecting Stations*: Nicaragua: Potosi and 5 miles SSW. of Monypenny Point, Gulf of Fonseca.

*Description*: Shell trigonally ovate, fairly thick, anterior side the longer, sloping and rounded at the end; posterior side with a fold, the end roundly truncated; ventral margin rounded; sculptured with fine close concentric riblets, on the anterior end these are decussated by several (10-15) incised radial lines; color pale yellowish-gray with purple blotches and ∧-shaped markings; pallial sinus higher in front of the adductor impression then gently sloping to a broadly rounded end which projects forward about three-fifths the length of the shell; hinge normal; interior colored white with the umbonal half and the hinge purple or tinged with purple.

A typical specimen from Nicaragua measures: length, 31 mm.; height, 25.4 mm.; convexity (both valves together), 12.5 mm.; pallial sinus projects anteriorly 19.8 mm. from the posterior margin of the shell.

The shells here referred to *Semele pulchra* agree exactly with the figures of that species given by Sowerby and by Reeve. *Semele quentinensis* Dall, a closely related species which has usually been cited under the name of *S. pulchra*, occurs from southern California to Central America. It is more elongate in outline, the anterior dorsal margin slopes more gently from the beaks, the shell is thinner and the purple coloration is more weakly developed.

*Distribution*: Only three specimens of this species were taken by the expedition in the Gulf of Fonseca. It ranges south to Ecuador.

### ***Semele quentinensis*** Dall.

Plate I, Fig. 10.

*Semele quentinensis* Dall, *West Amer. Sci.*, Vol. 19, No. 3, June 15, 1921, p. 22. "Pliocene or Early Pleistocene of San Quentin."—Dall, *Proc. U. S. Nat. Mus.*, Vol. 66, No. 2554, Art. 17, 1925, p. 26, pl. 8, fig. 4. "Pliocene (?) of San Quentin Bay, Lower California."

*Type Locality*: San Quintin, Lower California, Pleistocene.

*Range*: Point Mugu, Ventura County, California, to Costa Rica.

*Collecting Stations*: Guatemala: 7 miles west of Champerico (197-D-2), 14 fathoms, mud; El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell; Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves; Costa Rica: 1 mile south of Golfito.

*Description*: Shell small, inequilateral, inequivalve, rather compressed, anterior end longer, terminally rounded; posterior end obscurely subtruncate, base moderately arcuate; beaks inconspicuous; surface finely concentrically closely sculptured, with fine radial threads chiefly visible in the sulci; at the anterior end are about a dozen stronger sulci, cutting and more or less beading the concentric sculpture, but this feature is not

repeated at the posterior end; hinge normal, well developed; pallial sinus large, subovate, nearly reaching the anterior adductor scar, and entirely free from the pallial line; the left valve slightly flatter than the right valve. Length, 24; height, 19; diameter, 8 mm. (Original description).

A large specimen from the Gulf of Fonseca in the present collection measures: length, 27.3 mm.; height, 20.8 mm.; convexity (both valves together), 8.9 mm.; pallial sinus extends anteriorly 18 mm. from the posterior margin of the shell.

The shell of this species is very similar to that of *Semele pulchra* but the length is greater in proportion to the height and the anterior dorsal margin slopes more gently from the beaks. The specimens in the present collection are thinner and the purple coloration is less pronounced than that of *S. pulchra*. These shells possess fine, even, concentric sculpture which along the anterior dorsal margin is crossed by incised radial lines giving a beaded appearance to that portion of the shell. These specimens agree exactly with Dall's description and illustration of *Semele quentinensis* which was based on a fossil specimen from the Pleistocene of San Quintin, Lower California. These appear to be identical with the species occurring in southern California which generally has been cited in the literature under the name of *Semele pulchra*. The only difference seems to be in size, those from southern California seldom exceeding 20 mm. in length. A few specimens of this northern form also possess a few incised radial lines along the posterior dorsal margin but they are fewer and much weaker than those on the anterior dorsal margins and thus differ from the sculpture of *Semele jaramija* Pilsbry & Olssen which was originally described from the Pliocene of Ecuador. *Semele guaymasensis* Pilsbry & Lowe has more widely spaced and coarser concentric sculpture.

*Distribution*: Specimens of *Semele quentinensis* were dredged by the expedition in 12 to 16 fathoms from Guatemala to Costa Rica. It also is known to occur in the Pleistocene of southern California and Lower California.

### **Semele simplicissima** Pilsbry & Lowe.

*Semele simplicissima* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 93, pl. 12, figs. 6, 6a. "Acapulco, 20 fathoms."

*Type Locality*: Acapulco, Mexico, in 20 fathoms.

*Range*: Santa Inez Bay, Gulf of California, to Acapulco, Mexico.

*Collecting Stations*: Mexico: Arena Bank (136-D-2, 5), 33-45 fathoms, mud, *Arca* congomerates, sand, weed; Santa Inez Bay (143-D-2, 3, 4), 25-35 fathoms, mud, crushed shell; Santa Cruz Bay (195-D-21), 18 fathoms, mud; Costa Rica: Port Parker (203-D-3), 12 fathoms, shelly mud; 14 miles S. × E. of Judas Point (214-D-1, 4), 42-61 fathoms, mud, shell, rocks.

*Description*: Shell ovate, thin, moderately inflated at the umbos, beaks near the middle; anterior dorsal margin sloping, nearly straight, end rounded, ventral margin broadly rounded, posterior end a little higher than the anterior, convex dorsally, in large specimens decidedly truncated at the end where the fold reaches the margin; sculpture of very fine, fairly regular, low, concentric ridges which are covered by such fine, concentric lines that they disperse light into spectral colors; the interspaces are flat and without either concentric or radial striation; lunule lanceolate and rather deeply concave; pallial sinus ascending, rounded at the end and projecting a little beyond the middle of the shell; color dingy white and on the interior of fresh specimens a salmon pink or dark orange flush covers the umbonal half of the shell.

Some specimens in the present collection are much larger than the type of this species. The largest shell, a left valve, measures: length, 33 mm.; height, 24.3 mm.; convexity (one valve), 6.4 mm.; pallial sinus projects anteriorly 19 mm. from the dorsal margin of the shell. One pair of valves from Arena Bank measures, approximately: length, 29.5 mm; height, 22.8 mm.; convexity (both valves together), 12.2 mm.; pallial sinus extends anteriorly 16.5 mm. from the posterior margin of the shell.

The present specimens have been identified after a comparison with paratypes of *Semele simplicissima* in the H. N. Lowe collection in the San Diego Society of Natural History. This species appears to be very similar to the one described as *Semele regularis* Dall[21] [=*Semele paziana*, new name], but differs in that the intervals between the ribs are smooth and usually not ornamented by concentric striations. However, some specimens here referred to *S. simplicissima* bear submicroscopic striae in the interspaces.

*Semele sayi* Toula, 1909, described from the Gatun Miocene of Panama, and especially *S. quirosana* H. K. Hodson, 1931, described from the Upper Oligocene or Miocene of Venezuela, bear a resemblance to *S. simplicissima*.

*Distribution*: Specimens of this species were dredged by the expedition from Santa Inez Bay in the Gulf of California, to off Judas Point, Costa Rica, at depths of 12 to 61 fathoms. These records of occurrence furnish new extensions both north and south of the known range of the species.

### **Semele sparsilineata** Dall.

Plate I, Fig. 8.

*Semele sparsilineata* Dall, *Proc. Acad. Nat.*

[21] *Semele regularis* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, issued March 2, 1915, p. 27. "Gulf of California, off La Paz, in 10 to 30 fathoms."

Not *Semele regularis* E. A. Smith, Sci. Res. Voy. Challenger, Zool., Vol. 13, Lamell., 1885, p. 87, pl. 5, figs. 4, 4a, 4b. East of Cape York, North Australia in 155 fathoms.

A new name *Semele paziana* is here proposed for the west American species named *Semele regularis* by Dall.

*Sci. Philadelphia*, Vol. 67, issued March 2, 1915, p. 26. "Panama, 18 fathoms." Also recorded from "Chile, Hupé."

*Type Locality*: Panama, in 18 fathoms.

*Range*: Corinto, Nicaragua, to Taboga Island, Panama. To Chile (Dall).

*Collecting Station*: Panama: Gulf of Chiriqui (221-D-1, 5), 35-40 fathoms, sandy mud.

*Description*: Shell ovately oblong, the anterior portion much the longer, the end rounded, ventral margin rounded, posterior end slightly higher, slightly subtruncated, a flexure present; sculptured by fine concentric lines of growth which, sometimes anteriorly and sometimes medially, are crossed by fine oblique striations; pallial sinus ascending, broadly rounded at the end, projecting forward about three-fifths the length of the shell; color dingy white with traces of brownish-purple stains.

The larger specimen in the collection, a right valve, measures approximately: length, 25.5 mm.; height, 20.8 mm.; convexity (one valve), 4.7 mm.; pallial sinus extends anteriorly 15.8 mm. from the posterior margin of the shell.

The present specimens are somewhat worn but they show the oblique striae characteristic of this species. It was upon the basis of sparser oblique striae that Dall separated this species from the east American *Semele purpurascens* Gmelin[22].

*Distribution*: Only two single valves of this species were dredged by the expedition in the Gulf of Chiriqui, Panama, in 35-40 fathoms.

### **Semele tabogensis** Pilsbry & Lowe.

*Semele tabogensis* Pilsbry & Lowe, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 84, May 21, 1932, p. 91, pl. 12, figs. 5, 5a, 5b. "Taboga Island, among rocks near the bathing beach."

*Type Locality*: Taboga Island, Panama, among rocks.

*Range*: Tangola-Tangola Bay, Mexico, to Taboga Island, Panama.

*Collecting Station*: Mexico: Tangola-Tangola Bay (196-D-7), 6 fathoms, sand.

*Description*: The shell is thin, orange, shading through pink into light coral red near the umbones; very shortly oval, strongly compressed, slightly inequilateral. The broadly rounded anterior end is somewhat lower than the posterior end, which is noticeably truncate. Dorsal margin somewhat concave in front of the beaks, convex behind them. In the right valve these margins are produced towards the other valve, covering the ligament. Ventral margin is strongly convex. Sculpture of regular, recurved concentric riblets, which become laminar near the dorsal margin, and are somewhat darker colored than their intervals, in which fine, weak, radial striation is seen. Beaks smooth. Lunule extremely small, confined to the right valve. The interior varies in color from carnelian red to apricot orange, smooth, with some scattered glossy dots. Teeth are lighter or whitish in large individuals. Anterior lateral short, the posterior long and thinner. The pallial sinus reaches well past the middle. Length 37.5 mm., height 30.3 mm., semidiam. (right valve) 6.5 mm. (Original description).

The present specimen, a left valve, measures approximately: length, 22.3 mm.; height, 17.3 mm.; convexity (one valve), 4.3 mm.

*Distribution*: A single left valve of this species was dredged by the expedition in Tangola-Tangola Bay, Mexico, in 6 fathoms. This is an extension north of the known range of this species.

### **Semele venusta** Reeve.

Plate I, Fig. 13.

*Amphidesma venusta* Reeve, Conch. Icon., Vol. 8, *Amphidesma*, October, 1853, species 3, pl. 1, fig. 3. "Hab. West Columbia."—A. Adams, *Proc. Zool. Soc. London* for 1853 (issued July 25, 1854), p. 96. "Hab. West Columbia. Mus. Cuming."

*Type Locality*: West Colombia.

*Range*: Acapulco, Mexico, to west Colombia.

*Collecting Stations*: Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Santa Cruz Bay; Tangola-Tangola Bay (196-D-8), 9 fathoms, sand.

*Description*: Shell oblong, transverse, ventricose, rather shining, dull flesh-color, obscurely rayed with rose, anterior side much the longer, posterior slightly truncated, flexuous at the ventral margin; concentrically grooved; purple within, edged with white (Reeve).

A left valve in the present collection from Santa Cruz Bay, Mexico, measures: length, 21.9 mm.; height, 15 mm.; convexity (one valve), 4.2 mm.; pallial sinus extends anteriorly 14 mm. from the posterior margin of the shell.

The pallial sinus of this shell is a distinctive feature. It extends forward about two-thirds the length of the shell; it is broad and higher in front of the posterior adductor impression then tapers elliptically to a rounded point.

The ribbing of *Semele venusta* is somewhat irregular toward the anterior and posterior ends similar to that of *S. incongrua* Carpenter[23] athough coarser ventrally. The

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[22] *Venus purpurascens* Gmelin, Syst. Nat., ed. 13, Vol. 1, Pars. 6, 1791, p. 3288. Habitat unknown. Ref. to: "List. Conch. t. 303. f. 144."; "B (List. Conch. t. 304. f. 145."; "Klein. ostr. t. 11. f. 57".)

*Tellina obliqua* Wood, Gen. Conch., 1815, p. 152, pl. 41, figs. 4, 5.

This is not *Amphidesma purpurascens* Sowerby (Conch. Illustr., Pt. 19, species No. 19, pl. 18, fig. 5, issued between January 18 and March 8, 1833. "St. Elena. W. Col. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Sanctam Elenam." "A single valve of this elegant species was picked up on the sands at St. Elena".—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, November, 1853, species 37, pl. 6, fig. 37), which was renamed *Semele sowerbyi* by Lamy (*Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 18, No. 3, 1912, p. 165, footnote).

[23] *Semele incongrua* Carpenter, Rept. Brit. Assoc. Adv. Sci. for 1863 (issued August, 1864), pp. 611, 640. "Catalina

shell in adult forms is thicker than that of Carpenter's species. Fine radial sculpture is present in the bottoms of the interspaces.

A few small specimens in the present collection from off western Mexico are remarkably similar to *Semele incongrua*. Traces of the pallial sinus appear to be narrowly elliptical at the end similar to that of *S. venusta* rather than broady rounded as in *S. incongrua*.

The form described as *Semele pulchra* var. *montereyi* Arnold[24], based on a Pleistocene fossil from San Pedro, California, is, as mentioned by Dall, a subspecies of *S. incongrua*. The type specimen has not been illustrated but the figure given by Arnold represents a shell which appears to be a little more rounded, with sharper, more erect concentric lamellae and with stronger radial ornamentation than that of *S. incongrua*.

Verrill[25] considered *semele venusta* to be but a young form of *S. formosa* Sowerby. The pallial sinus, elliptically pointed in *S. venusta*, is quite different from the broadly rounded ascending pallial sinus of *S. formosa*.

*Distribution*: A few valves of *Semele venusta* were taken by the expedition at Port Guatulco, Santa Cruz Bay, and Tangola-Tangola Bay, Mexico, in 7 to 9 fathoms.

### **Semele verrucosa** Mörch.

Plate I, Figs. 21, 24.

*Semele* (*Amphidesma*) *verrucosa* Mörch, Malakozool. Blätter, Bd. 7, December, 1860, p. 190. "Los Bocorones ad prof. 20 org. spec. 2". Costa Rica.

*Type Locality*: Los Bocorones Islands, Costa Rica.

*Range*: Los Bocorones Islands, Costa Rica, to Hannibal Bank, Panama.

*Collecting Station*: Panama: Hannibal Bank (Sta. 224), 35-40 fathoms, rocks, coral, mud, sand, shells, algae.

*Description*: Shell elongately ovate, inequilateral, whitish blotched with purple; anterior side the longer, the end rounded, ventral margin broadly rounded, posterior end broadly rounded and with a gentle fold; sculpture consists of close concentric ribs, these especially anteriorly and posteriorly are wrinkled and give rise to scalloped scale-like projections, the whole finely radially wrinkled; hinge (right valve) with two cardinals and laterals; pallial sinus broadly rounded at the end and gently ascending to about five-eighths the length of the shell.

A right valve measures approximately: length, 43 mm.; height, 32.4 mm.; convexity (one valve), 7.1 mm.; pallial sinus extends anteriorly 26.6 mm. from the posterior margin of the shell.

Mörch pointed out that the shell of *Semele verrucosa* is more elongate in outline, more subtruncate posteriorly, and that the ventral margin is more gently arcuate in outline than that of *S. formosa* Sowerby[26]. The present specimen possesses those characters as well as the pronounced scaly verrucose sculpture characteristic of Mörch's species.

*Distribution*: A single right valve of this species was dredged by the expedition on Hannibal Bank, Panama, in 35-40 fathoms. This is an extension south of the known range of the species.

### Genus ***Abra*** Lamarck.

*Abra* Lamarck, Hist. Nat. Anim. s. Vert., Vol. 5, July, 1818, p. 492. Species cited: "*Amphidesma tenuis*" in the synonymy of which was included, "*Mactra tenuis*. Maton, act. soc. linn. 8. p. 72. no. 8" and "*Abra tenuis*. Leach". "Habite les mers d'Angleterre. Communiqué par M. Leach"; "*Amphidesma prismatica*" in the synonymy of which was cited, "*Ligula prismatica*. Montagu. test. brit. suppl. 23. t. 26. f. 3. Ex D. Leach." and "*Abra prismatica*. Leach." "Habite les côtes d'Angleterre. Communiqué par M. Leach."—Gray, *Proc. Zool. Soc. London* for 1847, p. 187. Type: *Mactra tenuis*.—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, 1900, p. 995. Type: *A tenuis* Montagu.—Woodring, *Carnegie Inst. Washington, Pub.* 366, 1925, p. 179. Type: *Mactra tenuis* Montagu.

*Type* (designated by Gray, 1847): *Mactra tenuis* [Montagu, Test. Brit., Pt. 2, 1803, p. 572, Suppl., 1808, pl. 17, fig. 7. "Southampton, where it is not uncommon on the shore to the west of the town." Also from "Weymouth"—Forbes & Hanley, Hist. Brit. Moll., Vol. 1, 1853 (issued 1848), p. 323, pl. 17, fig. 7. Various localities in England]. [For dates of publication of this work see Fisher and Tomlin, *Jour. Conch.*, Vol. 20, No. 5, August, 1935, pp. 150-151].

Shell small, trigonal; sculpture consisting of incrementals; ligament narrow, resilium seated on a wide, deeply inset chondrophore; hinge of right valve consisting of 2 cardinals (3a, 3b), the posterior one (3b) heavier, and slender anterior and posterior laterals; hinge of left valve consisting of 2 cardinals (2a, 2b), the posterior one (2b) very small; pallial sinus deep, very wide, confluent with pallial line (Woodring).

The genus *Abra* has been recorded as occuring from Eocene to Recent.

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Is., 40-60 fm.; common." Reprint in *Smithson. Miscell. Coll.*, No. 252, 1872, pp. 97, 126.—Carpenter, *Proc. California Acad. Nat. Sci.*, Vol. 3, February, 1865, p. 208 (as *Semele incungrua*). "Hab. Santa Barbara, 16 fm. 1 valve; Catalina Island, 40-60 fm., not uncommon; Cooper."—I. S. Oldroyd, *Stanford Univ. Publ. Univ. Ser. Geol. Sci.*, Vol. 1, 1924, p. 181, pl. 11, figs. 12, 13. "Type locality, Santa Barbara." Range, Monterey, California, to tbe Coronado Islands, Lower California.

[24] *Semele pulchra* Sowerby, var. *montereyi* Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 166, pl. 15, figs. 3, 3a. Lower San Pedro series, San Pedro, California. Pleistocene. Recent in Monterey Bay.

[25] Verrill, A. E., *Amer. Jour. Sci.*, Ser. 2, Vol. 69, No. 146, March, 1870, p. 219.

[26] *Amphidesma formosum* Sowerby, Conch. Illustr., Catal. issued with Pt. 19, No. 4, pl. 19, fig. 8 [two figs.], issued between January 18 and March 8, 1833. "St. Elena. Mr. Cuming."—Sowerby, *Proc. Zool. Soc. London* for 1832 (issued March 13, 1833), p. 199. "Hab. ad Sanctam Elenam." "Only two odd valves were dredged in seven fathoms water."—Reeve, Conch. Icon., Vol. 8, *Amphidesma*, 1853, species 27, pl. 4, fig. 27 (as *Amphidesma formosa*). Original locality cited.

Lamy[27] cited *Mactra tenuis* Montagu, the type of *Abra*, and similar species, under the genus *Syndesmya* Recluz, 1843, with the type *Mactra alba* Wood, 1801.

*Iacra* H. & A. Adams, 1856, a subgenus of *Abra*, with the type *Scrobicularia seychellarum* A. Adams, 1856, possesses divaricate radial sculpture.

*Abranda* Iredale, 1924, is based upon *Abranda rex* Iredale, an Australian species.

KEY TO THE SPECIES OF *Abra*.

A. Shell elongate
  a. Posterior end pointed ..... *pacifica*[28]
  aa. Posterior end blunt ..... *tepocana*[28]
B. Shell short; high, inflated ..... *palmeri*

### *Abra palmeri* Dall.

Plate I, Figs. 16, 18, 20, 23.

*Abra palmeri* Dall, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 67, March 2, 1915, p. 28. "Ballenas Lagoon on the west coast of Lower California; the Gulf of California (Dr. E. Palmer); and Panama Bay in 26 fathoms (U. S.N.Mus.). Type locality, Panama Bay. (U. S.N.Mus., No. 96,301.)"

*Type Locality*: Panama Bay, in 26 fathoms.

*Range*: Ballenas Lagoon on the west coast of Lower California, and the Gulf of California to Panama Bay.

*Collecting Station*: El Salvador: Meanguera Island, Gulf of Fonseca (199-D-1), 16 fathoms, sand, mud, crushed shell.

*Description*: Shell short, high, inflated, white, with a silky surface, and a very thin, polished, pale yellow periostracum; anterior end and base rounded; beaks subcentral, dorsal margins descending, posterior end attenuated and with the extremity rounded; right valve with a deeply bifid (or double) cardinal tooth, the laterals obsolete; left valve with a single cardinal and no laterals. Length 10, height 8, diameter 5.5. mm. The pallial sinus rounded, 6 mm. deep. (Original description).

This species is nearest to *A. lioica* Dall, of the Atlantic Coast of the United States (Dall).

The largest specimen in the present collection measures: length, 10.5 mm.; height, 9.2 mm.; convexity (one valve), 2.8 mm.

The short and high outline of *Abra palmeri* separates it from the two other species described from west American waters, *A. pacifica* Dall, 1915, and *A. tepocana* Dall, 1915, both of which were said to be elongate in outline.

*Distribution*: Several specimens of this species, mostly single valves, were dredged off Meanguera Island, El Salvador, in the Gulf of Fonseca, in 16 fathoms. This is the first record of the occurrence of the species since its original description.

[27] Lamy, E., *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, pp. 268-297.

[28] Not represented in the present collection.

## Genus *Cumingia* Sowerby.

### *Cumingia lamellosa* Sowerby.

*Cumingia lamellosa* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. prope littora Oceani Pacifici." "Found at Payta in hard clay at low water; and at Panama in deep water."—Sowerby, Gen. Rec. and Foss. Shells, *Cumingia*, Vol. 2, No. 40, ?1833, pl. 244, fig. 3.—Sowerby, Conch. Icon., Vol. 19, *Cumingia*, 1873, species 5, pl. 1, fig. 5. "Hab. Chili".— Lamy, *Journ. de Conchyl.*, Vol. 61, No. 3, 1914, p. 310. Paita, Peru.

*Cumingia coarctata* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. ad Sinum Caraccensem." "Dredged from a sandy muddy bottom in seven fathoms water in the Bay of Caraccas". [Ecuador].

*Cumingia trigonularis* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 35. "Hab. ad Sanctam Elenam." "Found among stones in deep water."—Sowerby, Gen. Rec. and Foss. Shells, Vol. 2, No. 40, ?1833, *Cumingia*, pl. 244, fig. 2.—Sowerby, Conch. Icon., Vol. 19, *Cumingia*, 1873, species 4, pl. 1, fig. 4. "Hab. Chili?"

*Cumingia adamsii* Carpenter, *Proc. Zool. Soc. London*, June 23, 1863, p. 367. Reprint in *Smithson. Miscell. Coll., No.* 252, 1872, p. 203. Name proposed for *Cumingia*, sp. indet. *c* of C. B. Adams, *Ann. Lyceum Nat. Hist. New York*, Vol. 5, July, 1852, p. 512 (separate p. 288). "Near Panama."

*Cumingia moulinsii* De Folin, Les Méléagrinicoles (Havre), 1867, p. 16, pl. 2, figs. 12, 13, 14, 15. . . . "l'Océan pacifique" . . . "pêchées aux environs des Negritos" . . . or . . . "autour des îles aux Perles, dans la baie de Panama".—De Folin & Périer, Les Fonds de la Mer, Vol. 1, 1867, p. 8. Bay of Panama. [For dates of publication of this work see H. A. Rehder, *Proc. Malacol. Soc. London*, Vol. 27, Pt. 2, September 5, 1946, pp. 74-75].

*Type Locality:* Paita, Peru, at low water, in hard clay (here designated as type locality). Panama, in deep water, also cited originally.

*Range:* San Martin Island, Lower California, to the Gulf of California and south to Paita, Peru.

*Collecting Stations:* Mexico: Port Guatulco (195-D-9), 7 fathoms, gr. sand, crushed shell; Nicaragua: Corinto (200-D-10, 16, 17, 19), 4-13 fathoms, mangrove leaves, sand, also on shore; Costa Rica: Port Parker.

*Description:* Shell oblong, regularly concentrically laminated, laminae narrow, standing out, distant; anterior side short, rounded; posterior side angular, acuminated, subrostrated; ventral margin contracted near the end; dorsal margin sloped (Sowerby, Conch. Icon., Vol. 19).

Some of the larger specimens in the present collection are about 12 mm. in length. Some specimens attain a length of 20 mm. or more.

*Cumingia lamellosa* lives in sand, sponges and in fissures in rocks. Consequently it

shows great variation in the shape of the shell and in the development of the lamellae. This variation has led to the publication of a number of different names for this species by various authors.

The more northern *Cumingia californica* Conrad, has a larger and thicker shell. *Cumingia similis* A. Adams is a synonym of Conrad's species.

*Cumingia mutica* Sowerby[29], which occurs in Peru and Chile, possesses a large shell for the genus. It is ornamented by finely decussated scupture. *Cumingia clerii* A. Adams[30], *C. grandis* Deshayes[31], *C. striata* A. Adams[32] and *C. ventricosa* Sowerby[33] were referred to the synonymy of *C. mutica* by Dall.

*Cumingia lamellosa* Sowerby is not to be confused with *Thyella lamellosa* H. Adams, 1885, described from the island of Mauritius, later renamed *Cumingia elegans* by Sowerby, 1873.

*Cumingia tellinoides* Conrad, 1831, *C. tellinoides coarctata* Sowerby, 1833, and *C. tellinoides vanhyningi* Rehder, 1939, occur in east American waters.

*Distribution:* Specimens of *Cumingia lamellosa* were taken by the expedition off western Mexico, Nicaragua and Costa Rica. Specimens questionably identified as this species have been recorded as occurring in the Pleistocene of Magdalena Bay, Lower California.

## Family Donacidae.

### Key to the Genera of the Donacidae.

A. Inner margin crenulated ..... *Donax*
B. Inner margin smooth ..... *Iphigenia*

## Genus **Donax** Linnaeus.

### Key to the Species of *Donax*.

A. Shell more than twice as long as high
  a. Anterior dorsal margin concave *transversus*
  aa. Anterior dorsal margin straight or convex
    b. Posterior dorsal area flattened or rounded
      c. Shell flattened; very elongate *gracilis*
      cc. Shell moderately inflated; higher ..... *californicus*
    bb. Posterior dorsal area concave; posterior area smoky-black; shell subrhomboidal ..... *navicula*
B. Shell less than twice as long as high
  a. Shell with a sharply angled umbonal carina posteriorly
    b. Thin; anterior end acutely rounded; highly polished ..... *carinatus*
    bb. Thick; anterior end more broadly rounded ..... *rostratus*[34]
  aa. Shell with a rounded umbonal angulation posteriorly; strongly sculptured
    c. Interspaces punctate (with a row of fine pits)
      d. Shell subtriangular (typical), high; posterior margin sloping rather steeply; ventral margin sometimes slightly expanded medially *punctatostriatus*
      dd. Shell elongate, lower; flatter; posterior margin sloping more gently, posterior end rostrate; base more broadly rounded
        e. Moderately elongated *contusus*[34]
        ee. Extremely elongated; posterior dorsal margin somewhat rounded *culter*[34]
    cc. Interspaces not punctate
      f. Length not exceeding 15 mm.; sculpture finely cancellate *obesus*
      ff. Length exceeding 15 mm.; sculpture coarsely cancellate; thick
        g. Beaks subcentral; shell high, trigonal
          h. Ribs on posterior area of about equal size ..... *asper*
          hh. Ribs on posterior area with 1-3 coarser than the others *dentiferus*[34]
        gg. Beaks decidedly posterior; shell more elongated *assimilis*

### **Donax asper** Hanley.

*Donax asper* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 14. "Hab. Tumbez, Peru (Cuming)."—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 12, pl. 2,

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[29] *Cumingia mutica* Sowerby, *Proc. Zool. Soc. London*, May 17, 1833, p. 34. "Hab. prope littora Maris Pacifici." Obtained "at Conception in seven fathoms, sand and mud; at Iquiqui in nine fathoms, gravel and mud; at Payta in hard clay at low water; and at Muerte."—Sowerby, Conch. Icon., Vol. 19, *Cumingia*, 1873, species 3, pl. 1, fig. 3. "Hab. Chili, Peru."

[30] *Cumingia clerii* A. Adams, *Proc. Zool. Soc. London*, November 12, 1850, p. 24, pl. 8, fig. 3. "Found at Talcuhano, Chili, by Capt. Clery, French Marine, attached to fuci in shallow water. (Mus. Cum.)."—Sowerby, Conch. Icon., Vol. 19, *Cumingia*, 1873, species 2, pl. 1, fig. 2. "Hab. Chili."

[31] *Cumingia grandis* Deshayes, *Journ. de Conchyl.*, Vol. 5, 1857, p. 281, pl. 8, figs. 4 and 5. . . . "provient des mers du Chili".—Sowerby, Conch. Icon., Vol. 19, *Cumingia*, 1873, species 11, pl. 2, fig. 11. "Hab. Chili".

[32] *Cumingia striata* A. Adams, *Proc. Zool. Soc. London*, November 12, 1850, p. 25, pl. 8, fig. 5. "Hab. Conception; seven fathoms, sandy mud; H. C. (Mus. Cuming)."

[33] *Cumingia ventricosa* Sowerby, Conch. Icon., Vol. 19, August, 1873, species 10, pl. 2, fig. 10. "Hab. Probably Chili."

[34] Not represented in the present collection.

fig. 12. Original locality record cited.—Sowerby, Thes. Conch., Vol. 3, 1866, p. 307, pl. 280 (*Donax*, pl. 1), fig. 24. Tumbez, Peru.

*Donax* (*Hecuba*) *asper* Hanley, Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 14, Tab. 3, figs. 7-10. Tumbez, Peru; Puntarenas, Costa Rica, in the Gulf of Nicoya.

*Donax aspera* Hanley, Dall, *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, pp. 159, 273, pl. 28, fig. 7. Central America to Tumbez, Peru.

*Type Locality:* Tumbez, Peru.

*Range:* Tangola-Tangola Bay, Mexico, to Tumbez, Peru.

*Collecting Stations*: Mexico: Tangola-Tangola Bay; Costa Rica: Port Culebra, beach; Culebra Bay; Cedro Island, Gulf of Nicoya, beach; Gulf of Dulce, beach; Panama: Bahia Honda.

*Description:* Shell triangular, beaks subcentral, elevated, and rather gibbous; the anterior end is rather acutely rounded, the posterior end somewhat concavely truncated; ornamented by radiating riblets which are especially well developed toward the posterior end and on the posterior area where they are crenated by concentric lines; inner margin crenulated; the color is ashy-white or purple.

A large right valve in the present collection from the Gulf of Dulce measures, approximately: length, 35 mm.; height, 26 mm.; convexity (one valve), 8.5 mm.

Compared to *Donax assimilis* Hanley, the shell of *D. asper* is much higher in proportion to the length and the beaks are much more centrally located. The shell of *D. asper* differs from that of *D. dentiferus* Hanley[35] in that it is thicker, more acutely rounded anteriorly and lacks the raised ribs (1-3) which are coarser than the others on the posterior area of that species.

*Distribution*: This species was collected by the expedition from Mexico to Panama but nowhere in large numbers. Several single valves were taken on the beach in the Gulf of Dulce, Costa Rica, and at Tangola-Tangola Bay, Mexico.

### **Donax assimilis** Hanley.

*Donax assimilis* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 17. "Hab. Panama. Mus. Cuming, Hanley, &c."—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 10, pl. 2, fig. 10. Panama.

*Donax panamensis* Philippi, *Zeit. f. Malakozool.*, Jahrg. 5, No. 10, 1848, p. 145. "Patria: Panama." [According to Römer, 1869, this species is a synonym of *D. assimilis*.]

*Donax cayennensis* Lamarck, Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 22, pl. 4, figs. 22a, 22b. "Hab. Panama and St. Elena, West Columbia; Cuming."

Not *Donax caianensis* Lamarck, Anim. S. Vert., Vol. 5, July, 1818, p. 550. "Habite l'Océan de la Guyane."—Delessert, Rec. Coq. décrites par Lamarck et non encore figurées, 1841, pl. 6, figs. 13a, 13b. See also Hanley, Cat. Rec. Biv. Shells, 1843, p. 82, footnote.—Lamy, *Bull. Mus. Nat. Hist. Nat.* (Paris), Vol. 20, No. 6, 1914, p. 339.

*Donax reevei* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 85. [Name based upon Reeve's pl. 2, fig. 10. Panama (Reeve).]

*Donax sowerbyi* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 85, pl. 4, figs. 2a, 2b, 2c. Based upon Sowerby's (Thes. Conch., Vol. 3, 1866, p. 307), pl. 280 (*Donax*, pl. 1), fig. 21. "Panama."

*Type Locality:* Panama.

*Range:* Mazatlan, Mexico (Carpenter), to Santa Elena, Ecuador.

*Collecting Stations:* Nicaragua: Isla Encantada, Corinto; Costa Rica: Culebra Bay; Cedro Island, Gulf of Nicoya, beach; Gulf of Dulce, beach; Panama: Isla Parida, Gulf of Chiriqui.

*Description:* Shell elongately triangular, beaks posterior to the middle, anterior end the narrower, rounded, posterior end truncated; ornamented with radial riblets which are stronger toward the posterior end and on the posterior area which sometimes bears a faint subangulation; inner margin crenated; color, usually some shade or combination of gray and purple.

A large specimen of this species in the collection of the California Academy of Sciences, collected by James Zetek at Chame Island, Panama, measures: length, 41 mm.; height, 26.8 mm.; convexity (both valves together), 17.5 mm.

Compared to *Donax asper* the shell of *D. assimilis* is much more elongate, the beaks are more posteriorly situated and the posterior area is more rounded. The more posteriorly situated beaks and more elongated shell are characters which serve to separate the present species from *D. dentiferus*.

*Distribution:* This species was taken by the expedition on the beach at a few localities from Nicaragua to Panama. It occurs commonly at Panama where it is used for food by the natives.

### **Donax californicus** Conrad.

Plate I, Figs. 2, 5.

*D*[*onax*]. *californica* Conrad, *Jour. Acad. Nat. Sci. Philadelphia*, Vol. 7, 1837, p. 254, pl. 19, fig. 21. "Inhabits the coast of California in sand, near Sta. Barbara."

Not *Donax californica* Conrad, Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 40, pl. 6, fig. 40. "Hab. Gulf of California." [Carpenter, 1855, referring to some of the shells in the Gulf of California region labeled as *D. californicus*, stated, "The shells wrongly called *D. californicus* are simply the white variety of the forms *contusus* and *culter*"].

*Donax californicus* Conrad, Arnold, *Mem. Calif. Acad. Sci.*, Vol. 3, 1903, p. 170, pl. 13,

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35 *Donax dentifera* Hanley, *Proc. Zool. Soc. London*, Pt. 11, July, 1843, p. 6. "Hab.—?"—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 2, pl. 1, figs. 2a, 2b. "Hab. Panama."

fig. 9. Lower San Pedro Series at Deadman Island, and San Pedro, California. Lower Pleistocene. Also upper Pleistocene and Recent.—Weymouth, State of Calif. Fish & Game Comm., *Fish Bull.* No. 4, 1920, p. 47, pl. 16, fig. 1. Localities cited from San Pedro to False Bay, California.

*Type Locality:* Near Santa Barbara, California, in sand.

*Range:* Santa Barbara, California, to Magdalena Bay, Lower California.

*Collecting Station:* Mexico: Cedros Island, Lower California.

*Description:* Shell elongated, somewhat pointed at both extremities; disks with very minute radiating lines; color yellowish, obscurely rayed; a brown stripe on the anterior and posterior sub-margin; within white and purplish brown; margin beautifully crenulated. (Original description.)

A specimen of this species in the collections of the California Academy of Sciences, collected by Henry Hemphill at Cape San Lazaro, Lower California, measures: length, 24.6 mm.; height, 11 mm.; convexity (both valves together), 7.4 mm.; from beaks to posterior end, 10 mm. Large specimens attain a length of about 30 mm.

*Donax californicus* can be referred to the subgenus *Serrula* Chemnitz in Mörch.

The posterior dorsal area of the shell of this species is flattened or gently rounded rather than concave as in *D. navicula.*

*Donax gracilis* Hanley is a similar southern species whose shell is more elongated and whose posterior dorsal margin slopes more gently ventrally.

*Distribution:* A few small specimens of *Donax californicus* were dredged off Cedros Island by the expedition. We have not seen specimens from south of Cape San Lazaro, Lower California[36]. It is also known to occur in the Pleistocene of southern California and western Lower California.

### **Donax carinatus** Hanley.

Plate I, Fig. 9.

*Donax carinata* Hanley, *Proc. Zool. Soc. London,* Pt. 11, July, 1843, p. 5. "Hab. —? Mus Stainforth, Metcalfe." — Hanley, Cat. Rec. Bivalve Shells, p. 84, 1843, p. 349, pl. 14, fig. 28, 1856 (as *Donax carinatus* on expl. to plate). [No locality cited.]—Reeve, Conch. Icon., Vol. 8, *Donax,* September, 1854, species 11, pl. 2, fig. 11. "Hab. San Blas, California."

*Donax carinatus* Hanley, Sowerby, Thes. Conch., Vol. 3, 1866, p. 305, pl. 280 (*Donax,* pl. 1), figs. 4 and 5. "California."—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae,* 1869, p. 10, Taf. 3, figs. 4, 5, 6. "Fundort: Der Stille Ocean bei Californien, (St. Blas, Tumaco, Mazatlan)."

*Donax culminatus* Carpenter, Cat. Mazatlan Shells, September, 1855, p. 43. "Hab. — 1 young specimen; L'pool Col."

*Type Locality:* San Blas, Mexico (here designated as type locality). No locality cited originally.

*Range:* Altata, Mexico, to Tumaco, Colombia.

*Collecting Station:* Nicaragua: Corinto (200-D-16, 19), 4-13 fathoms, mangrove leaves.

*Description:* Transversely elongated, convex, very inequilateral, purplish-brown, with more or less distinct radiating striae, (usually with obsolete darker rays and polished), ventral edge little arcuated and forming a very acute point with the nearly straight edge of the obliquely truncated and almost flattened anterior [posterior] slope, which is sharply carinated and sculptured by close decussated radiating striae: inside purple, two lateral teeth in each valve, the ventral edge crenated, anterior crenulated. 4/5 . . . 1 2/5 [inches] (Hanley, Cat. Rec. Biv. Shells, 1843).

The largest specimen in the present collection measures 33.2 mm. in length and 18 mm. in height. A large right valve collected by the senior author at Corinto, Nicaragua, measures approximately: length, 39.4 mm.; height, 22 mm.; convexity (one valve), 7.6 mm.

This species can be easily recognized by the comparatively thin, polished shell with a sharply angled umbonal ridge posteriorly.

The only other west American shell that might be confused with *Donax carinatus* is *Donax rostratus* C. B. Adams[37]. The shell of Adams' species is thicker, less sharply carinated, and is less sharply pointed where the carina joins the ventral margin, the anterior end is more broadly rounded, and the color of the exterior is lighter.

A subspecies, *Donax carinatus galvestonensis* Harris[38], has been described from an artesian well in Galveston, Texas, and was considered to be of upper Miocene age. Harris did not consider Reeve's plate 2, figure 11, as representing Hanley's species.

*Distribution:* This species was dredged by the expedition off Corinto, Nicaragua, at depths of 4-13 fathoms. It also has been collected by the senior author at Corinto and at Mazatlan, Mexico. Römer cited the occurrence of the species as far south as Tumaco, Colombia.

### **Donax gracilis** Hanley.

Plate I, Figs. 4, 6.

*Donax gracilis* Hanley, *Proc. Zool. Soc. London,* Pt. 13, April, 1845, p. 15. "Hab. Bay of Guayaquil. Var. *b.* Chiriqui. Var. *c.* Bay of Caraccas (Cuming)." — Reeve, Conch.

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[36] According to Miss Viola Bristol, specimens of this species from Magdalena Bay, Lower California, are in the collections of the San Diego Society of Natural History (*Min. Conch. Club South. Calif.,* No. 47, back page, April, 1945). On the same page of this paper Eyerdam is cited as having found this species at Corinto, Nicaragua.

[37] *Donax rostratus* C. B. Adams, *Ann. Lyceum Nat. Hist. New York,* Vol. 5, July, 1852, pp. 502, 545 (separate pp. 278, 321). "Panama."—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae,* 1869, p. 11, Taf. 3, figs. 1-3.

[38] *Donax carinata* var. *galvestonensis* Harris, *Bull. Amer. Paleo.,* Vol. 1, No. 3, December 2, 1895, p. 92 (10). Well at Galveston, Texas, depth, 2,552 to 2,920 feet. Upper Miocene.

Icon., Vol. 8, *Donax*, September, 1854, species 38, pl. 6, fig. 38. "Hab. Gulf of Guayaquil; Cuming."—Sowerby, Thes. Conch., Vol. 3, 1866, p. 314, pl. 282 (*Donax*, pl. 3), figs. 76, 77, 78, 79. Gulf of Guayaquil.—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 80, Taf. 14, figs. 4, 5, 6. [?7, 8]. "Fundort: Der Stille Ocean bei Mittelamerika und Ecuador, (Guayaquil, Chiriqui, Panama)."

*Type Locality:* Bay of Guayaquil, Ecuador (here selected as type locality). Chiriqui [Panama] and Bay of Caraccas [Ecuador] also cited originally for varieties of this species.

*Range:* Lat. 24° 18′ N., west coast of Lower California, to the Gulf of California and south to Negritos, Peru.

*Collecting Station:* Nicaragua: Corinto (200-D-10, 11, 16, 17, 19), 7-13 fathoms, sand, mangrove leaves, also in beach drift.

*Description:* Shell narrowly elongate, polished, rather compressed, beaks nearer the posterior end; anterior end acutely rounded, posterior end acutely roundly pointed; posterior dorsal margin straight or slightly produced; inner margin finely crenulated; color of the exterior is usually brown and that of the interior brownish-purple.

A large left valve from off Potosi and Monypenny Point, Nicaragua, measures approximately: length, 22.5 mm.; height, 9.4 mm.; convexity (one valve), 3 mm.; distance from beak to posterior end, 9 mm.

The shell of *Donax gracilis* differs from that of *D. navicula* in the much more elongate outline and in that the posterior dorsal margin is straight or slightly produced rather than concave. Compared to *D. californicus* the shell of *D. gracilis* is longer in proportion to the height, more compressed, the posterior dorsal margin slopes more gently and the posterior end is more acutely pointed. It can be referred to the subgenus *Serrula*.

*Donax punaensis* Pilsbry & Olsson[39], described from the Pliocene of Ecuador, is a very similar species but the beaks appear to be more centrally situated and the posterior end is more broadly rounded.

*Donax petersoni* Olsson, described from the Oligocene of Peru, is a somewhat similar species.

*Donax owenii* Gray in Hanley[40] of the Atlantic fauna appears to be somewhat similar to *D. gracilis* but the posterior end appears to be shorter and the margin is said to be smooth not crenulated.

*Distribution:* Specimens of *Donax gracilis* were taken by the expedition in the beach drift as well as dredged in 7 to 13 fathoms at Corinto, Nicaragua.

### **Donax navicula** Hanley.

Plate I, Fig. 1.

*Donax navicula* Hanley, *Proc. Zool. Soc. London*, Pt. 13, April, 1845, p. 15. "Hab. Gulf of Nicoya, Central America (Cuming)".—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 18, pl. 4, fig. 18. Original locality cited.—Sowerby, Thes. Conch., Vol. 3, 1866, p. 314, pl. 282 (*Donax*, pl. 3), fig. 80. Original locality cited.—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 56, Taf. 10, figs. 1-3. "Fundort: Der Stille Ocean bei Californien und Mittelamerika, (Nicoyia, Panama, Mazatlan, Reallejos)."

*Type Locality:* Gulf of Nicoya, Costa Rica.

*Range:* Gulf of California to Panama.

*Collecting Stations:* Mexico: Santa Inez Bay, Gulf of California; Cape San Lucas; Cape San Lucas Bay; Nicaragua: Potosi and Monypenny Point, Gulf of Fonseca; Corinto (200-D-10, 16), 4-7 fathoms, mangrove leaves, also in beach drift.

*Description:* Shell elongately rhomboidal, moderately inflated, fairly thick, obsoletely, finely radially grooved; anterior end the longer, acutely rounded, posterior end acuminately truncated, the extremity roundly pointed; posterior area concave; ventral margin rounded and somewhat expanded just anterior to the middle, often with a compressed area between this portion of the valve and the posterior angulation; inner margin crenulated; color white or brownish with the posterior and anterior dorsal areas black or grayish-black; periostracum greenish.

One of the largest specimens, a right valve, from the beach drift at Corinto, Nicaragua, measures approximately: length, 21 mm.; height, 10 mm.; convexity (one valve), 3.9 mm.; distance from beaks to posterior end, 8.5 mm.

The shell of *Donax navicula* differs from that of *D. gracilis* in the more rounded base and rhomboidal form, more inflated valves and especially in that the posterior area is concave. It can be referred to the subgenus *Serrula*.

The concave posterior area and higher more triangular form are features which serve to separate *Donax navicula* from *D. californicus*.

*Distribution:* This species was taken abundantly by the expedition in the beach drift at Corinto, Nicaragua. A few specimens were also taken as far north as Santa Inez Bay in the Gulf of California.

### **Donax obesus** d'Orbigny.

Plate I, Fig. 7.

*Donax obesa* d'Orbigny, Voy, Amér.

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39 *Donax punaensis* Pilsbry & Olsson, *Proc. Acad. Nat. Sci. Philadelphia*, Vol. 93, September 9, 1941, p. 72, pl. 12, fig. 2. "Pliocene of the north end of Puna Island." Ecuador.

40 *Donax owenii* Gray in Hanley, Cat. Rec. Bivalve Shells, 1843, p. 81. "Africa?"—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 37, pl. 6, fig. 37. "Hab. West Coast of Africa."

Dall (*Nautilus*, Vol. 5, No. 4, August, 1891, p. 44), recorded this species from Montevideo and Maldonado. Maury (Serv. Geol. & Min. Brasil, Mon. No. 4, 1924, p. 455) also cited the species as occurring at Montevideo, Uruguay. Melvill & Standen recorded a species under the name of *Donax* (*Machaerodonax*) *owenii* Gray, from Karachi, India (*Proc. Zool. Soc. London*, November 13, 1906, p. 826). Carcelles recently cited *Donax owenii* as occurring along the coast of Argentina (Rev. Mus. de La Plata (New Ser.), Sec. Zool., Vol. 3, 1944, p. 303).

Mérid., Vol. 5, 1846, p. 541, pl. 81, figs. 28, 30. "Elle a été pêchée à Payta (Pérou) par M. Fontaine."—Reeve, Conch. Icon., Vol. 8, *Donax*, October, 1854, species 49, pl. 7, fig. 49. "Hab. Real Llejos, Central America; Cuming."

*Donax obesus* d'Orbigny, Sowerby, Thes. Conch., Vol. 3, 1866, p. 310, pl. 281 (*Donax*, pl. 2), figs. 42, 43. "Real Llejos, Central America."

*Type Locality*: Paita, Peru.

*Range*: Corinto, Nicaragua, to Paita, Peru.

*Collecting Station*: Nicaragua: Corinto (200-D-11, 19), 8-13 fathoms, mangrove leaves.

*Description*: Shell small, subtriangular, inflated; the anterior end the longer, sloping, acutely rounded at the extremity, posterior end broadly and roundly truncated; umbonal ridges rounded; ornamented with fine radial grooves which are crossed by somewhat flexuous concentric grooves forming a fine cancellated pattern of punctate appearance; inner margin finely crenulated; color white with dark purplish-brown on the posterior end and on the anterior dorsal margin.

The largest specimen in the collection, a right valve, measures: length, 13.4 mm.; height, 10.9 mm.; convexity (one valve), 4.2 mm.

The shell of *Donax obesulus* Reeve[41] is much more abruptly truncated than that of *D. obesus*, and the posterior umbonal ridge is decidedly angulated rather than rounded.

*Distribution*: This species was dredged by the expedition at two localities off Corinto, Nicaragua, at depths of 8-13 fathoms.

### **Donax punctatostriatus** Hanley.

Plate I, Fig. 17.

*Donax punctato-striata* Hanley, *Proc. Zool. Soc. London*, Pt. 11, July, 1843, p. 5. "Hab.—? Mus. Stainforth, Metcalfe, Hanley, &c."—Hanley, Cat. Rec. Biv. Shells, 1843, p. 84, pl. 14, fig. 24 (as *Donax punctato-striatus* on expl. to plate). [Not the record "China"].—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 16, pl. 3, figs. 16a, 16b. "Hab. Mazatlan, Gulf of California."—Sowerby, Thes. Conch., Vol. 3, *Donax*, 1866, p. 310, pl. 281 (*Donax*, pl. 2), figs. 49, 50 (as *Donax punctato-striatus*). Reeve's locality cited on expl. to pl.

*Type Locality*: Mazatlan, Mexico (here designated as type locality). No locality cited originally.

*Range*: San Ignacio Lagoon, Lower California, to the Gulf of California and south to Negritos, Peru.

*Collecting Stations*: Mexico: Santa Inez Bay, Gulf of California; Cape San Lucas; Chamela Bay; Tenacatita Bay; Sihuatanejo; Tangola-Tangola Bay; Nicaragua: Gulf of Fonseca; Potosi and Monypenny Point; Corinto (200-D-19), 12-13 fathoms, mangrove leaves, also beach.

*Description*: Subtriangular, very convex, pale livid brown, with strong radiating punctated striae, becoming very fine and close on the anterior [posterior] slope, whose edge is rounded, posterior and anterior edges much sloping, ventral arcuated in the middle; inside stained with violet, the ventral margins dentated, the anterior [posterior] crenulated: two cardinal and lateral teeth in each valve. Long. 4/5—1-1/5 [inches] (Hanley, Cat. Rec. Biv. Shells, 1843). "When full grown less inequilateral than most of this genus."

A very large specimen of this species in the Henry Hemphill collection in the California Academy of Sciences, collected at Magdalena Bay, Lower California, measures: length, 44.8 mm.; height, 30 mm.; convexity (both valves together), 17.4 mm.

The subtrigonal form and the row of fine pits, which occur in the radial grooved striae, are characteristic features of this species. It belongs to the subgenus *Chion* Scopoli.

Hanley once reported *Donax punctatostriatus* from China but it was later recognized as occurring commonly in tropical west American waters.

The variety described by Carpenter as *Donax punctatostriatus* var. *caelatus*[42] appears not to have been recognized since its description. It was described as possessing short impressed lines rather than pits in the interspaces.

Sowerby (1866) pointed out that there are specimens which intergrade between *Donax punctatostriatus* and *Donax conradi* Reeve[43]. The latter species is now known to be identical with *D. contusus* Reeve[44] (see our Pl. I, fig. 14), as pointed out by Tomlin[45]. *Donax vellicata* Reeve (fig. 66) and *D. bitincta* Reeve (fig. 68), both described without information as to the locality from which they came, are likewise identical with *D. contusus* according to Tomlin.

Typical forms of *Donax punctatostriatus* are more subtrigonal and higher than those of typical *D. contusus*, which are lower and more elongate in outline. Large specimens of *D. punctatostriatus* are sometimes slightly expanded medially along the ventral margin and the posterior dorsal margin often slopes more steeply than that on *D. contusus*, but as mentioned by Sowerby, there is intergradation between the two forms. The most elongate form of this variable group is *Donax*

[41] *Donax obesula* Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 30, pl. 5, fig. 30. "Hab. Peru."—Deshayes, *Proc. Zool. Soc. London*, 1854 (issued May 16, 1855), p. 352. "Hab. Central America."

[42] *Donax ?punctatostriatus*, var. *caelatus* Carpenter, Cat. Mazatlan Shells, September, 1855, p. 46. "Hab.—Mazatlan; very rare."

[43] *Donax conradi* Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 29, pl. 5, fig. 29. "Hab. Gulf of California."

[44] *Donax contusus* Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 24, pl. 4, fig. 24. "Hab. Mazatlan, Gulf of California."

[45] Tomlin, J. R. leB., *Nautilus*, Vol. 40, No. 2, October, 1926, p. 52.

*culter* Hanley[46], as pointed out by Carpenter[47]. Very elongate forms of *D. culter* are somewhat reminiscent of *Amphichaena kindermanni* Philippi[48] as is *Donax petallinus* Reeve[49].

*Donax aricanus* Dall[50], recorded as occurring from Paita, Peru, to Arica, Chile, appears to be very similar to *D. punctatostriatus* and possibly some of the records of the occurrence of the latter species in South America may be referable to Dall's species. Römer considered *D. radiatus* Valenciennes [=*aricanus*] to be only a variety of *D. punctatostriatus*.

*Donax striatus* Linnaeus, which occurs in the Caribbean region, is a similar species.

*Distribution*: This species was collected by the expedition on the beach and dredged at depths of 12-13 fathoms, from Santa Inez Bay in the Gulf of California to Corinto, Nicaragua. It is a variable shell found commonly from the Gulf of California to Peru. It has been recorded as occurring in the Pleistocene of southern California, Magdalena Bay, Lower California, and at Oaxaca, Mexico.

### **Donax transversus** Sowerby.

Plate I, Fig. 3.

*Donax transversa* Sowerby, Cat. Shells Tankerville, 1825, Ap., p. IV. [No locality cited].—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 36, pl. 6, fig. 36. "Hab.—?"

*Donax transversus* Sowerby, Sowerby, Thes. Conch., Vol. 3, 1866, p. 306, pl. 280 (*Donax*, pl. 1), fig. 11. "Hab.—?"—Carpenter, Cat. Mazatlan Shells, September, 1855, p. 44. Mazatlan, Mexico.

*Type Locality*: Corinto, Nicaragua (here designated as type locality). No locality cited originally.

*Range*: Mazatlan, Mexico, to San Juan del Sur, Nicaragua.

*Collecting Station*: Nicaragua: Corinto (200-D-19), 12-13 fathoms, mangrove leaves.

*Description*: "D. testâ transversim elongatâ, laevi; latere postico brevi, biangulato, carinato, obliquè truncato, longitudinaliter sulcato; extus albidâ; fulvo obsoletè radiatâ". (Original description).

The shell of this species is very elongated, very inequilateral, rather thin, moderately inflated, gaping at each end, polished and obsoletely radially striated; anterior dorsal margin slightly concave; anterior end elliptically rounded obliquely joining the slightly rounded ventral margin; posterior end truncated, set off by a carina, the area fairly broad, concave, with a faint rounded angulation medially, the whole area finely radially striated and at the end obliquely truncated; color yellowish-white with purple rays; ventral margin finely crenated.

Specimens of this species in the present collection are small. A large left valve collected at Corinto, Nicaragua, by the senior author measures: length, 36.4 mm.; height, 14.5 mm.; convexity (one valve), 4.5 mm.; distance from beak to posterior end, 14 mm.

This appears to be the species which authors have cited from western Mexico and Central America under the name of *Donax scalpellum* Gray. *Donax scalpellum* Gray[51] was originally described without information as to locality. Hanley[52] later cited it from "California" and Reeve[53] cited it from the Gulf of California. E. A. Smith[54] in 1891 cited it from Aden, in the Gulf of Aden, and stated: "The above named locality, given by Reeve (Conch. Icon. sp. 39), has never been confirmed, and I think there is little doubt that it is incorrect. The specimens from Aden agree in form, color, sculpture, and every other respect with that figured by Reeve." Later Melvill & Standen[55] cited the species as occurring at Karachi, India, in the Arabian Sea.

The concavity of the anterior dorsal margin, obliquely elliptically rounded anterior end, and much wider and radially striated posterior area are features separating *Donax transversus* from *D. scalpellum*. *Donax transversus* belongs to the subgenus *Machaerodonax* Römer, the type of which is *D. scalpellum* Gray.

*Distribution*: Three small specimens of *Donax transversus* were dredged by the expedition in 12-13 fathoms off Corinto, Nicaragua. It also has been collected by the senior author on the beach at the same locality.

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46 *Donax culter* Hanley, *Proc. Zool. Soc. London*, April, 1845, p. 14. "Hab. Var. a. Matzellan [Mazatlan] Gulf of California (Cuming). Var. b. Acapulco (Cuming)."—Reeve, Conch. Icon., Vol. 8, *Donax*, September, 1854, species 21, pl. 4, fig. 21. "Hab. Gulf of California."

47 Carpenter, P. P., Cat. Mazatlan Shells, September, 1855, pp. 47-48.

48 See Palmer, R. H., and Hertlein, L. G., *Bull. South. Calif. Acad. Sci.*, Vol. 35, Pt. 2, May-August (issued September 10), 1936, p. 71, pl. 18, figs. A, B, C, pl. 19, figs. 5, 6, 7, 8, 9, 10. Mazatlan; Petatlan Bay; Tenacatita Bay, Mexico, Recent. Also Oaxaca, Mexico, Pleistocene.

49 *Donax petallina* Reeve, Conch. Icon., Vol. 8, *Donax*, October, 1854, species 51, pl. 8, fig. 51. "Hab.—?"—Deshayes, *Proc. Zool. Soc. London* for 1854 (issued May 16, 1855), p. 350 (as *Donax petalina*). "Hab.—? Coll. Cuming."

This species was described without information as to the locality from which it came. Bertin (*Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 84), stated that he found an indication in Deshayes' collection that the species came from Chile. Dall, 1909, and Gigoux, 1934, also cited it from that country. Pilsbry & Lowe, 1932, and Bales, 1938, cited it from Acapulco, Mexico.

50 *Donax radiata* Valenciennes, Rec. d'Obser. Zool. Humboldt & Bonpland, Vol. 2, 1832, p. 221, pl. 1, figs. 3a, 3b, 3c, 4. "Habitat in Oceano Pacifico ad Americae calidioris litora." Not *Donax radiata* Gmelin, 1791.

*Donax aricana* Dall, *Proc. U. S. Nat. Mus.*, Vol. 37, November 24, 1909, p. 273. New name for *Donax radiata* Valenciennes, 1832, not *D. radiata* Gmelin, 1791. Paita, Peru, to Arica, Chile.

51 *Donax scalpellum* Gray, *Ann. Philos.*, Vol. 25, February, 1823, p. 136. [No locality cited].—Wood, Index Test., Suppl., 1828, p. 4, pl. 2, *Donax*, fig. 1. [No locality cited].

52 Index Test. by W. Wood, edit. by S. Hanley, 1856, p. 202, Suppl. pl. 2, *Donax* fig. 1. "California."

53 Reeve, L. A., Conch. Icon., Vol. 8, *Donax*, September, 1854, species 39, pl. 6, fig. 39. "Hab. Gulf of California."

54 Smith, E. A., *Proc. Zool. Soc. London*, 1891, p. 427.

55 Melvill, J. C., and Standen, R., *Proc. Zool. Soc. London*, November 13, 1906, p. 826.—Melvill, *Proc. Malacol. Soc. London*, Vol. 18, Pt. 3, 1928, p. 115.

Genus **Iphigenia** Schumacher.

*Iphigenia* Schumacher, Essai Nouv. Syst. Test., 1817, pp. 51, 155. Sole species, *Iphigenia laevigata* (*Donax laevigata* Chemnitz.). Ref. to Chemnitz, Vol. 6, p. 253, pl. 25, fig. 249. Illustrated by Schumacher on pl. 17, figs. 4a, b.—Dall, *Trans. Wagner Free Inst. Sci.*, Vol. 3, Pt. 5, 1900, p. 962. Type: *Donax laevigata* Chemnitz.—Pilsbry & Bequaert, *Bull. Amer. Mus. Nat. Hist.*, Vol. 53, Art. 2, May 9, 1927, p. 369. *Donax laevigata* "Chemnitz" Gmelin accepted as type.

*Type* (by monotypy): *Donax laevigata* Chemnitz [Neues Syst. Conchyl.-Cab., Bd. 6, 1782, p. 253, Tab. 25, fig. 249. "Es wohnet diese Muschel in den ostindischen Meeren. Bey Tranqueber wird sie nur selten gefunden". Also illustrated by Schumacher, pl. 17, fig. 4a, b].

Shell large, subtriangular, subequilateral, without radial sculpture; thick, with entire ventral margins; two cardinals, the larger bifid, in each valve and two obsolete laterals in the right valve. (Dall).

The genus *Iphigenia* is known to occur in the Miocene of Venezuela and Peru. At the present time it often occurs in estuarine or brackish water conditions and is known to occur in greatest abundance from the coast and rivers of West Africa and from the tropical Atlantic and Pacific coasts of Central and South America. *Iphigenia centralis* Germain, an African species, ranges from the middle Niger river to strongly saline waters. One species occurs on the coast of Florida and one species occurs in tropical west American waters.

**Iphigenia altior** Sowerby.

*Capsa altior* Sowerby, *Proc. Zool. Soc. London*, Pt. 2, for 1832 (issued March 13, 1833,) p. 196. "Hab. in Peruviâ et Americâ Centrali." "Dredged among coarse gravel, in twelve fathoms water, in the Gulf of Nocoiyo. A smaller variety, which is also rather higher, was found at Tumbez, at a depth of five fathoms, in thin mud."—Hanley, Cat. Rec. Bivalve Shells, p. 86, 1843, pl. 14, fig. 34, 1844, p. 349, 1856. Peru and Central America.—Römer, Syst. Conchyl.-Cab. Martini-Chemnitz, Bd. 10, Abt. 3, *Donacidae*, 1869, p. 114, Tab. 21, figs. 1-4. Earlier records cited.

*Iphigenia ambigua* Bertin, *Nouv. Arch. Mus. Hist. Nat.* (Paris), Ser. 2, Vol. 4, 1881, p. 120, pl. 4, figs. 4a, 4b, 4c . . . "habite l'océan Pacifique, sur les côtes de l'Amérique centrale."

*Iphigenia altior* Sowerby, Dall, *Proc. U. S. Nat. Mus.*, Vol. 37, 1909, p. 159, pl. 25, fig. 8. Capon to Tumbez, Peru. Range, Gulf of California to Tumbez, Peru.

*Type Locality*: Gulf of Nicova, Costa Rica, in 12 fathoms, coarse gravel. Tumbez, Peru, also cited originally for a small variety of this species.

*Range*: Gulf of California to Tumbez, Peru.

*Collecting Stations*: Mexico: Chamela Bay, beach; Nicaragua: Potosi and Monypenny Point; Corinto, beach; Costa Rica: Port Culebra; Culebra Bay; Golfito Bay; one mile south of Golfito Bay.

*Description*: Shell subtriangular, the anterior side the longer, thick, moderately inflated, base rounded, anterior dorsal margin gently arcuate and sloping, rounded at the end, posterior dorsal margin more steeply sloping, more flattened and subtruncated at the end, a slight depression often present anterior to the posterior umbonal ridge; smooth except for lines of growth and submicroscopic radiating striae; two cardinal teeth in each valve, the right posterior and left anterior bifid or medially grooved; inner margin smooth; pallial sinus extends for about five-eighths the length of the shell, rounded at the end, and along the base for about a third of its length confluent with the pallial line; color yellowish or purplish-white under an olive periostracum, the umbos dark, the interior white and violet.

A very large right valve in the present collection from one mile south of Golfito Bay, Costa Rica, measures: length, 79 mm.; height, 57.3 mm.; convexity (one valve), 18 mm.; pallial sinus extends anteriorly 45 mm. from the posterior margin of the shell. A specimen in the collection of the California Academy of Sciences collected in Panama Bay by F. M. Anderson, measures: length, 68 mm.; height, 51.5 mm.; convexity (both valves together), 31 mm.; pallial sinus extends anteriorly 39 mm. from the posterior margin of the shell.

The specimen described as *Iphigenia ambigua* by Bertin may be slightly longer in proportion to the height as compared to some specimens of *I. altior*. In the absence of any other differences and in view of the variation shown in a series of shells, we have placed Bertin's species in the synonymy of *I. altior*. Carpenter[56] mentioned an elongate specimen from Mazatlan with a strong posterior ventral sinus which he referred to "*Iphigenia ?laevigata*, ?cujus." According to Carpenter, Gray considered the specimen to be an abnormal variety of *I. altior*. In general features *I. altior* is quite similar to *I. laevigata*, the type of the genus, from West Africa.

Compared to *Iphigenia brasiliana* Lamarck, which occurs in the Caribbean region, the shell of *I. altior* is considerably higher proportionately from beak to base and it has a much fainter depression anterior to the posterior truncation.

*Distribution*: Specimens of *Iphigenia altior* were collected by the expedition on beaches from Chamela Bay, Mexico, to Golfito Bay, Costa Rica. Dall mentioned that this species was found at a depth of 4 to 6 inches in sand, on flats and tidal lagoons of Peru.

[56] Carpenter, P. P., Cat. Mazatlan Shells, September, 1855, p. 42.

## EXPLANATION OF THE PLATE.

Fig. 1. *Donax navicula* Hanley. Hypotype, left valve, from Corinto, Nicaragua. Length, 18.8 mm.; height, 9.2 mm. P. ....

Fig. 2. *Donax californicus* Conrad. Hypotype, left valve, from San Pedro Bay, California. Length, 22 mm.; height, 9.8 mm. P. ....

Fig. 3. *Donax transversus* Sowerby. Hypotype, left valve, from Corinto, Nicaragua. Length, 36.6 mm.; height, 14.5 mm. P. ....

Fig. 4. *Donax gracilis* Hanley. Hypotype, left valve, from Potosi and 5 miles west of Monypenny Point, Nicaragua. Length, 22 mm.; height, 9.7 mm. P. ....

Fig. 5. *Donax californicus* Conrad. View of right valve of the specimen shown in Fig. 2.

Fig. 6. *Donax gracilis* Hanley. Hypotype, left valve, from Loc. 27588 (C.A.S.), about 13 miles southeast of Cape Tosco, Santa Margarita Island, west coast of Lower California. Collected by the Templeton Crocker Expedition, 1932. Length, 15.8 mm.; height, 7.3 mm. P. ....

Fig. 7. *Donax obesus* d'Orbigny. Hypotype, left valve, from Station 200-D-19, Lat. 12° 28′ 03″ N., Long. 87° 12′ 39″ W., Corinto, Nicaragua, in 12-13 fathoms (22-24 meters). Length, 11.1 mm.; height, 8.9 mm. P. ....

Fig. 8. *Semele sparsilineata* Dall. Hypotype, left valve, from Station 221-D-1, Lat. 7° 54′ 45″ N., Long. 82° 04′ 32″ W., Gulf of Chiriqui, Panama, in 35 fathoms (64 meters). Length, 22 mm.; height, 17.4 mm. P. ....

Fig. 9. *Donax carinatus* Hanley. Hypotype, left valve, from Corinto, Nicaragua. L. G. Hertlein, coll. Length, 36.3 mm.; height, 18.2 mm. P. ....

Fig. 10. *Semele quentinensis* Dall. Hypotype, right valve, from Station 199-D-1, Lat. 13° 08′ N., Long. 87° 43′ W., Meanguera Island, Gulf of Fonseca, El Salvador, in 16 fathoms (29 meters). Length, 26.4 mm.; height, 21.1 mm. P. ....

Fig. 11. *Semele pacifica* Dall. Hypotype, right valve, from Golfito, Gulf of Dulce, Costa Rica. Length, 19.4 mm.; height, 15.4 mm.

Fig. 12. *Semele jaramija* Pilsbry & Olsson. Hypotype, left valve, from Santa Inez Bay, Lower California, in the Gulf of California, on shore. Length, 16.1 mm.; height, 12 mm. P. ....

Fig. 13. *Semele venusta* Reeve. Hypotype, right valve, from Station 196-D-8, Lat. 15° 45′ 37″ N., Long. 96° 05′ 54″ W., Tangola-Tangola Bay, Mexico, in 9 fathoms (16.3 meters). Length, 17.8 mm.; height, 13 mm. P. ....

Fig. 14. *Donax contusus* Reeve. Hypotype, left valve, from Loc. 27230 (C.A.S.), Petatlan Bay, Mexico, about 6 miles south of Sihuatanejo. L. G. Hertlein, coll. Length, 39.1 mm.; height, 20 mm. (Illustrated for comparison with *Donax punctatostriatus*, Fig. 17). P. ..... (in text).

Fig. 15. *Semele pulchra* Sowerby. Hypotype, right valve, from Potosi and 5 miles SSW. of Monypenny Point, Nicaragua. Length, 31 mm.; height, 26 mm. P. ...

Fig. 16. *Abra palmeri* Dall. Hypotype, right valve, from Station 199-D-1, Lat. 13° 08′ N., Long. 87° 43′ W., Meanguera Island, Gulf of Fonseca, El Salvador, in 16 fathoms (29 meters). Length, 9.8 mm.; height, 9 mm. P. ....

Fig. 17. *Donax punctatostriatus* Hanley. Hypotype, left valve, from Loc. 4859 (C.A.S. H. Hemphill coll.), Magdalena Bay, Lower California. Length, 44.4 mm.; height, 28 mm. P. ....

Fig. 18. *Abra palmeri* Dall. View of the interior of the specimen shown in Fig. 16.

Fig. 19. *Semele craneana* Hertlein & Strong, sp. nov. Holotype, left valve, dredged in the Gulf of California. (Exact station unknown but probably in the southern portion of the Gulf of California). Length, 38 mm.; height, 29.5 mm. View of the interior. P. ....

Fig. 20. *Abra palmeri* Dall. Hypotype, left valve, from Station 199-D-1, Lat. 13° 08′ N., Long. 87° 43′ W., Meanguera Island, Gulf of Fonseca, El Salvador, in 16 fathoms (29 meters). Length, 10.5 mm.; height, 9.3 mm. View of the interior. P. ....

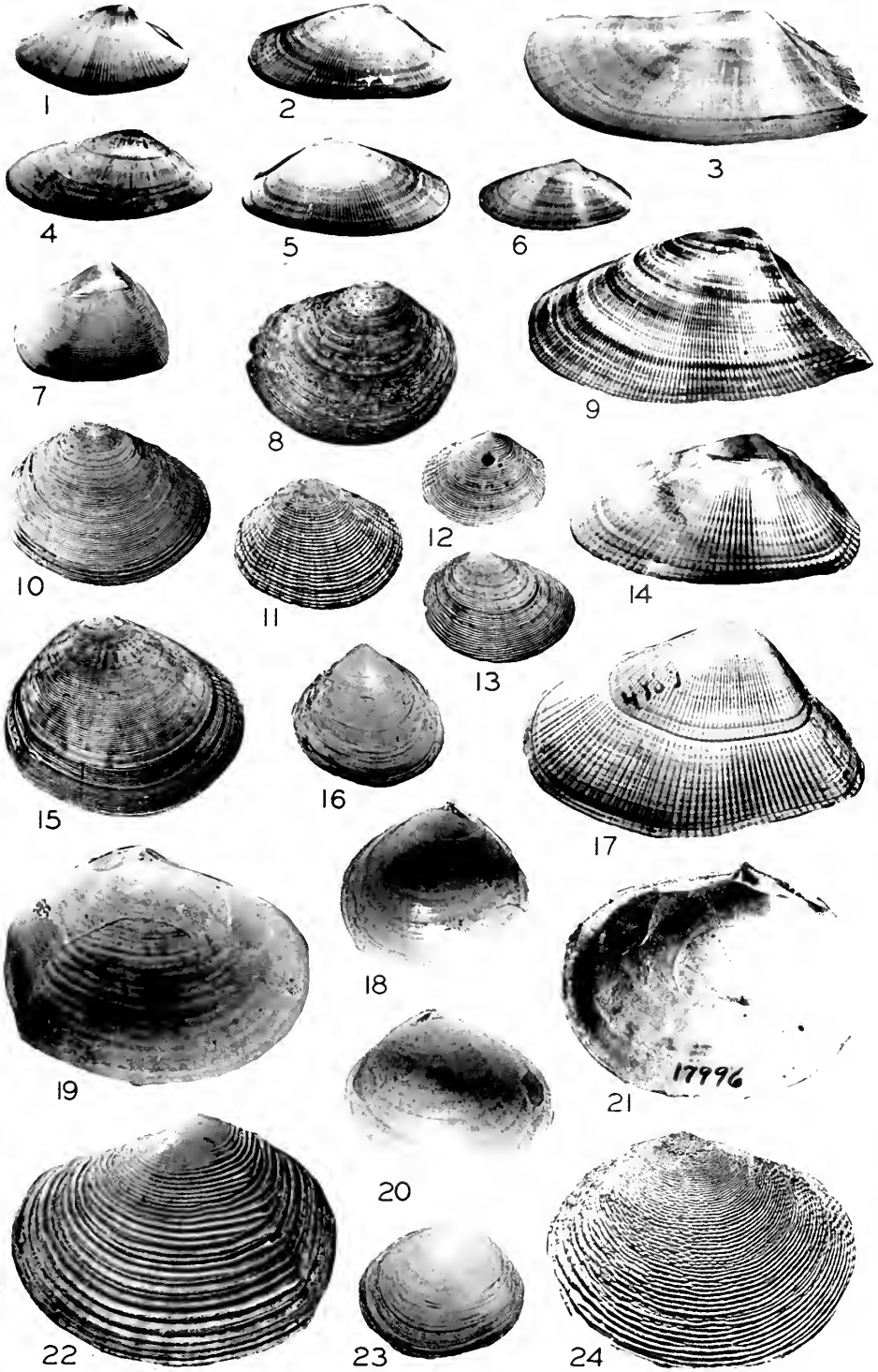
Fig. 21. *Semele verrucosa* Mörch. Hypotype, right valve, from Station 224, Lat. 7° 23′ 30″ N., Long. 82° 03′ W., Hannibal Bank, Panama, in 35-40 fathoms (64-73 meters). Length, 43 mm.; height, 32.8 mm. View of the interior. P. ....

Fig. 22. *Semele craneana* Hertlein & Strong, sp. nov. Holotype. View of the exterior of the specimen shown in Fig. 19.

Fig. 23. *Abra palmeri* Dall. View of the exterior of the specimen shown in Fig. 20.

Fig. 24. *Semele verrucosa* Mörch. View of the exterior of the specimen shown in Fig. 21.

All the specimens illustrated on this plate are in the type collection of the Department of Paleontology of the California Academy of Sciences.




MOLLUSKS FROM THE WEST COAST OF MEXICO AND CENTRAL AMERICA. PART VIII

# 20.

## Tettigellidae and Gyponidae (Homoptera) of Kartabo, Bartica District, British Guiana.

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(Text-figures 1-8).

[This contribution is a result of various expeditions of the Department of Tropical Research of the New York Zoological Society to British Guiana during the years 1917, 1919, 1920, 1921, 1922 and 1924, under the direction of Dr. William Beebe. For maps and ecological data refer to *Zoologica*, Vol. VI, 1925, pp. 1-193.]

CONTENTS.



### INTRODUCTION.

In 1945 the writer (Metcalf, 1945b) reviewed the Fulgoroidea from Kartabo collected by Dr. William Beebe and his associates. Included with these were a small number of leafhoppers belonging to the groups Tettigellidae (fomerly Cicadellinae) and Gyponidae. While the number of species in the present collection is not large, they are of sufficient interest to be worth reporting. A number apparently belong to species previously described and in these cases I have attemped to redescribe and illustrate these so as to bring them into line with modern taxonomic practices. A disproportionate number of species are apparently new. This number, however, does not seem to be out of line with the apparent number of new species from other parts of the world where, likewise, only incidental collections of these small and often inconspicuous insects have been made. No species has been described as new, nevertheless, until a thorough search has been made of the literature and careful comparisons made with the original descriptions of these species. As is well known to the students of these groups, the older descriptions are often totally inadequate. The writer is under no delusions as to his ability to place these older species accurately from the descriptions. However, since so many of these types are not readily available, the best the modern taxonomist can do is to try to correlate these older described species with the material at hand.

For the present the writer proposes to treat these two groups, Tettigellidae and Gyponidae, along with some other groups of leafhoppers, as families. Whether they are coordinate with other families of Homoptera or with families in other orders has not as yet been determined. But until the groups of the Homoptera have been studied more thoroughly, it is deemed best to treat them as distinct families of the superfamily Iassoidea.

### Family TETTIGELLIDAE.

Most of the species of this family are large or medium sized leafhoppers, very few are small. The body is cylindrical or more or less fusiform. The head is usually large and in a few species is produced into a definite cephalic process. The anteclypeus is large. The lora conspicuous. The postclypeus large, sometimes inflated, definitely projected onto the crown, facial portion usually with distinct transverse ridges. The lateral postclypeal sutures usually extending to the crown. Crown large, usually distinctly triangular in outline. Cephalic process sometimes distinct, short, triangular or elongate

terete. Paired ocelli on the crown remote from the anterior border of crown. Pronotum usually large, flat, more or less quadrangular in outline; anterior margin usually broadly curved; posterior margin usually broadly incised; lateral margins usually distinct. Mesonotum small, triangular. Tegmina elongate, usually narrow, coriaceous; venation usually distinct, sometimes strongly reticulate apically. Radius with two distinct branches; media unbranched; cubitus 1 unbranched, joined to the claval suture (cubitus 2) by a short but usually distinct cross vein. Usually two, (sometimes three or more) radial-medial cross veins and one (sometimes two) medial-cubital cross vein. Thus there is formed usually two (sometimes three) basal cells, two or three ante-apical cells and four or five apical cells, with the ante-apical and apical cells sometimes strongly reticulate. Wings transparent with a distinct submarginal vein which is incomplete on the costal margin. Radius with two branches, the first incomplete. Media with two branches. Media 1 plus 2 with a distinct radial cross vein and media 3 plus 4 with a distinct cubital cross vein. Cubitus 1 unbranched.

Subfamily TETTIGELLINAE.

Head, including compound eyes, usually narrower than the pronotum. Antennal ledges indistinct, not conspicuously separated from the coronal portion of the postclypeus. Lateral margins of the pronotum divergent caudad; or rounding, not distinctly separated from posterior lateral margins. Anterior tibiae not sulcate or expanded. Tegmina broader, usually covering the lateral margins of the abdomen.

***Erythrogonia*** Melichar, 1926a:373.

Orthotype *Erythrogonia laeta* Fabr.

The species of this genus are generally small slender tettigellids with the head including the eyes wider than the pronotum. The tegmina elongate, narrow with nearly parallel sides.

Crown shorter than the greatest width between the eyes; the ocelli usually on the posterior half; face somewhat angled to the crown, strongly impressed. Pronotum usually about as long as the crown, width usually greater than the median length. Mesonotum large. Legs slender. Tegmina elongate, rounded at the apex with three elongate ante-apical cells and three shorter apical cells.

***Erythrogonia bicolor*** n. sp.

Text-fig. 1 A-E.

This species closely resembles *Tettigonia rutilans* Walker (*Tettigonia carminata* Signoret) in general coloration but differs as follows: the apical margin of the tegmina translucent, not blackish, and the head, more elongate. Since neither the male nor female genitalia of *rutilans* have been described and since the head characters of the present species are decidedly different, together with the fact that *rutilans* has been recorded only from Brazil, it is believed to be better to describe this as a new species.

Crown about as long as broad, slightly impressed from the posterior lateral margins around the anterior margin, leaving the anterior margin as a broad slightly elevated border; ocelli on a line with the anterior margin of the compound eyes; face strongly produced, longer than its greatest width. Pronotum as long as crown, about one and a half times as broad as the median length; the anterior margin broadly curved; the posterior margin nearly straight; mesonotum large, nearly as long as pronotum.

Female last ventral segment four times as long as the penultimate, longer than broad, curvingly acuminate to the obtuse apex with a distinct median carina. The male genitalia with the genital plates with a broad base, slender, triangular acuminate apex about half as long as the pygofers; the pygofers when viewed ventrad, elongate, triangular, gradually acuminate from the base to the apex, not as long as the anal segment; when viewed laterad, broad with the apex broadly rounded; genital styles short, acuminate, broadly curved outward. Aedeagus shorter than pygofers with a strongly developed dorsal lobe and two elongate acuminate spines at the apex.

This is a small slender species with the head including the compound eyes, the pro- and mesonotum, and the basal angle of the tegmina blackish fuscous. Beneath, including the legs and abdomen, blackish fuscous. Tegmina bright red with the venation brown. Wings transparent with scarlet red veins. Crown black, almost as long as its width between the compound eyes.

Length to apex of tegmina: 9.75 mm.

Holotype: ♂ Kartabo, Bartica District; May 10, 1924. Allotype: ♀ Kartabo, Bartica District; July 4, 1922. Paratypes: 1 ♂ July 4, 1922; 1 ♂ May 10, 1924; 3 ♀♀ May 10, 1924.

***Amblyscarta*** Stål, 1869a:71.

Logotype *Amblyscarta modesta* Fabr.

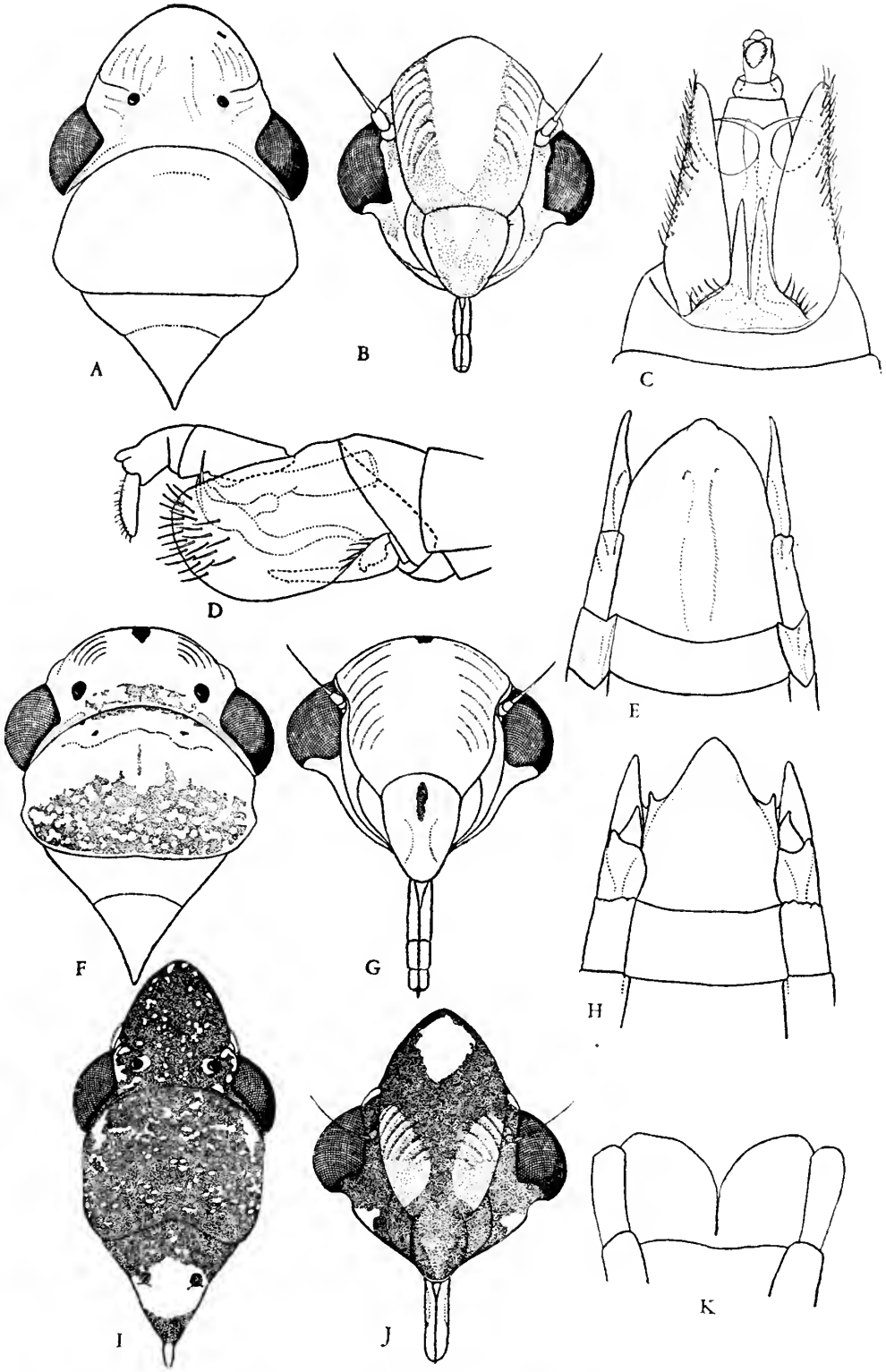
In this genus the head is broader than the pronotum. The crown is short and broad, length on the median line more than half the width between the eyes, broadly rounded to the face; face somewhat elongate. Pronotum about twice as long as the crown. Mesonotum large, almost as broad as the pronotum. Tegmina elongate, apical margin somewhat obtuse; anterior tibiae with a distinctly ciliated inner margin.

***Amblyscarta aurulenta*** Fabr.

(*Cicadella aurulenta* Osborn, 1926b:199).

(Text-fig. 1 F-H).

This common and well-known species is apparently widely distributed in South America, having been previously recorded from British, French and Dutch Guiana, Bolivia and Matto Grosso and Rio de Janeiro, Brazil. There are numerous specimens in the




TEXT-FIG. 1. *Erythrogonia bicolor*: **A**, head thorax; **B**, face; **C**, male genitalia ventral; **D**, male genitalia lateral; **E**, female genitalia. *Amblyscarta aurulenta*: **F**, head thorax; **G**, face; **H**, female genitalia. *Orectogonia flavoscutellata*: **I**, head thorax; **J**, face; **K**, female genitalia.

present collection from Kartabo, Bartica District, British Guiana.

While the color is quite variable, the head, pronotum and mesonotum are chiefly ochraceous orange with the legs and venter bright yellowish, the abdomen usually carmine red. The tegmina vary considerably in color and color markings. More typical specimens in the present collection have the basal third of the tegmina velvety brown with numerous irregular light bluish spots, the apex testaceous brown, the posterior border of the crown irregularly irrorate with brownish and the posterior third of the pronotum usually marked like the tegmina with a broad brownish band more or less irregularly spotted with light bluish. The brown spot at the apex of the head usually distinctive.

Female with the last genital segment more than twice as long as the penultimate, projecting caudad in a broad triangular lobe; the lateral margins usually projecting as a pair of small lateral teeth.

Length to apex of tegmina: 9.5-11.0 mm.

### **Orectogonia** Melichar, 1926a:345.

Logotype *Orectogonia sparsuta* Sign.

This is one of the genera established by Melichar in his key that has never been fully described. It may be characterized as follows: head including the compound eyes broader than the pronotum; crown elongate, conical, flat with the disc distinctly impressed with a very faint longitudinal furrow on the median line. Face somewhat inflated. Pronotum large, lateral margins parallel; anterior margin broadly curved; posterior margin triangularly incised. Mesonotum large, nearly as broad as pronotum. Caudal area distinctly produced. Tegmina translucent; venation distinct with three ante-apical and four apical cells, the fourth apical cell elongate. Legs short and slender, posterior tibiae with about six short stout spines on the outer margin; the anterior margin with numerous slender hairs, those on basal half short, those on apical half elongate, posterior margin with numerous short hairs.

### **Orectogonia flavoscutellata** Signoret.

(*Tettigonia flavoscutellata* Signoret, 1855c:509).

(Text-fig. 1 I-K.)

This species is apparently very close to *Orectogonia sparsuta* Sign., but it differs decidedly in coloration and in size.

Crown longer than the width between the eyes, the median impressed line rather indistinct. Ocelli large, close to compound eyes. Face strongly inflated; anteclypeus small. Pronotum slightly wider than long. Mesonotum large, distinctly bi-impressed behind the middle. Tegmina elongate, rather narrow; venation distinct, the ante-apical cells nearly three times as long as the apical cells. Claval veins distinct. Legs short and slender.

Female genitalia with the last ventral segment elongate, deeply incised on the posterior border, the incision almost reaching the anterior margin of the segment.

General color of the head, including the compound eyes and the thorax, blackish with numerous small round spots, yellowish or pale bluish-green, with a few larger irregular spots on the crown and the pronotum, and a large central area on the mesonotum, pale yellowish. Tegmina translucent, the veins blackish. Beneath general color blackish with a large median yellowish spot on the apex of the face and a pair of large yellowish spots at base of antennae, irregular yellowish spots on the sides of the thorax and the venter of the abdomen. Legs chiefly yellow with the posterior tibiae and the base of the posterior tarsi chiefly blackish.

Length to the apex of the tegmina: 11 mm.

Single female specimen from Kartabo, Bartica District, British Guiana, March 18, 1922.

## Subfamily PROCONIINAE.

Head, including compound eyes, usually broader than the pronotum. Antennal ledges distinct, projecting, conspicuously separated from the coronal portion of the postclypeus. Lateral margins of the pronotum usually parallel. Anterior tibiae sulcate or expanded toward the apex. Tegmina narrow, not covering the lateral margins of the abdomen.

### **Acrocampsa** Stål.

(Melichar, 1925a:337).

Haplotype *Fulgora pallipes* Fabr.

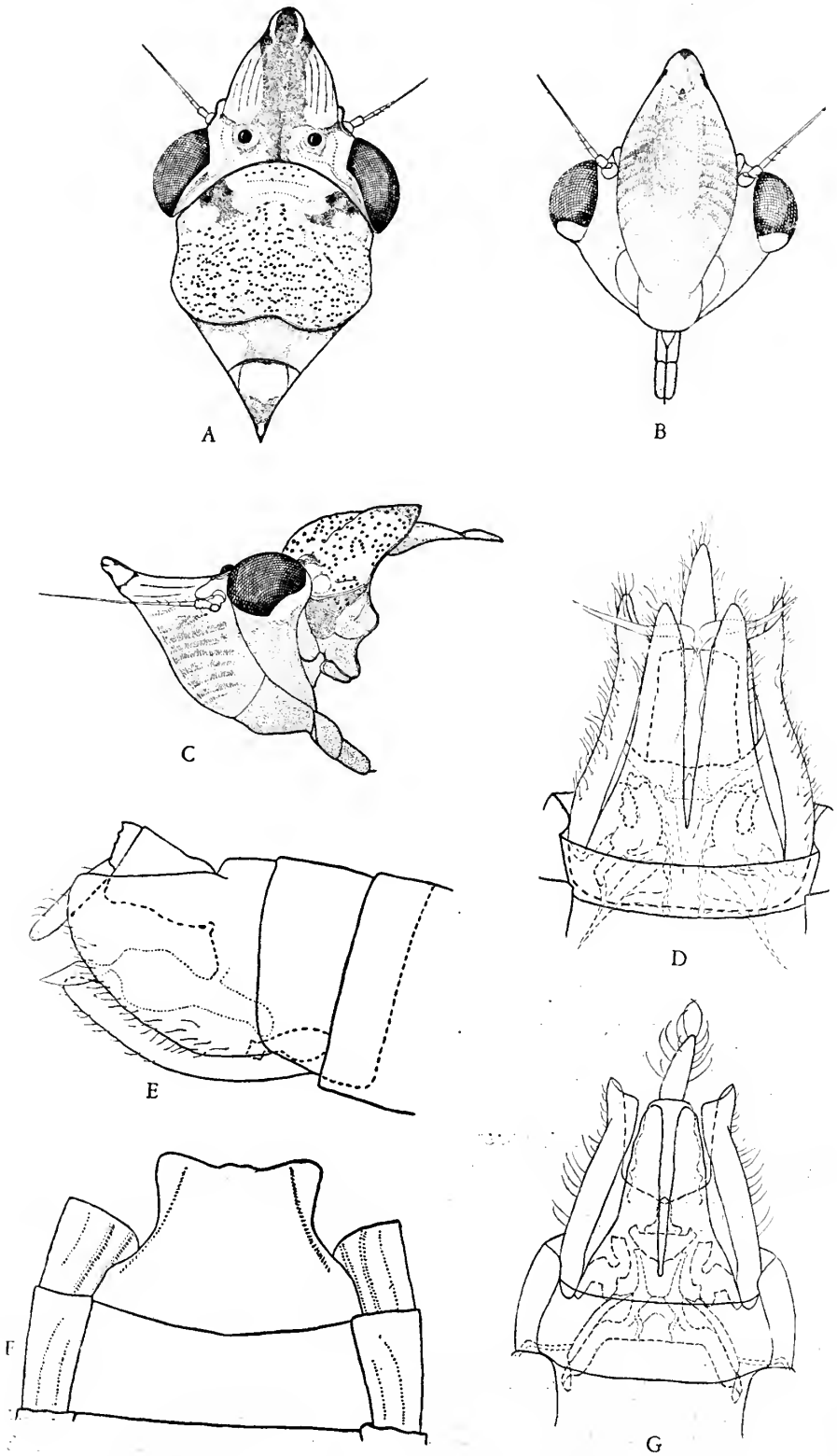
Head including the compound eyes wider than the pronotum; crown suddenly constricted in front of the compound eyes, then broadly triangularly produced to the apex which is slightly upturned. Apex with a deep longitudinal furrow both above and below. Face strongly produced; anteclypeus viewed laterad somewhat angular. Pronotum narrow with the sides parallel; anterior margin broadly curved; separated into two distinct parts — the anterior part depressed, about the same level as the crown; posterior part strongly elevated, trilobed. Mesonotum broad, not very long; apex produced into a rather slender process. Anterior tibiae broadened at the apex; posterior tibiae elongate, nearly twice as long as the femora, with a few rather stout spines on the anterior and posterior ventral margins; basitarsi not longer than the two apical segments. Tegmina rather narrow, coriaceous; venation not very distinct; the whole surface finely rugulose. Costal and commisural margins nearly parallel: apical margin obtuse.

### **Acrocampsa pallipes** Fabr.

(*Fulgora pallipes* Fabricius, 1787a:261).

(Text-fig. 2 A-F).

This species may be readily distinguished from *Catorthorrhinus resimus* by the following combination of characteristics and distinctive coloration:




TEXT-FIG. 2. *Acrocampsa pallipes*: **A**, head thorax; **B**, face; **C**, lateral head thorax; **D**, male genitalia ventral; **E**, male genitalia lateral; **F**, female genitalia. *Acrocampsa rufa*: **G**, male genitalia ventral.

Crown somewhat longer than greatest width between the eyes, equalling the pronotum in length; cephalic process short, broadly rounded, deeply impressed, semi-erect; ocelli large, projecting; compound eyes large; face elongate, nearly twice as long as greatest width; postclypeus nearly elliptical in outline; median impression on face deep.

Female last ventral segment broad, not quite twice as broad as median length; caudal area nearly quadrangular; posterior margin shallowly incised with a median third broadly produced with a median incision at the apex. Male genitalia last ventral segment short and broad, nearly four times as broad as its median length; genital plates nearly as long as pygofer; aedeagus elongate with pair of elongate, slender, acute apical processes.

Length to apex of tegmina: 13.5 mm.

**Acrocampsa rufa** Melichar.

(Melichar, 1925a:339).

(Text-fig. 2 G).

This species may be recognized by the following points: crown, pronotum and mesonotum chiefly yellowish, more or less clouded with light brown. Tegmina chiefly bright reddish-brown, base usually greenish-fuscous; apex transparent bordered with blackish basad. Beneath, including the legs and venter of the abdomen, chiefly pale ochraceous.

Male genitalia last ventral segment about three times as broad as its median length; genital plates slightly shorter than pygofers, obtuse; aedeagus less than half as long as genital plates.

Length to apex of tegmina: 13.5 mm.

**Dichrophleps** Stål.

(Melichar, 1925a:327).

Haplotype *Cicada aurea* Fabr.

This genus has recently been reviewed by Melichar. He describes this genus and gives a key to the species including *aurea* Fabr. The species of this genus are quite variable in color markings and it is by no means certain that there is more than one species in Central and South America.

Head, including compound eyes, broader than pronotum; crown flat. Anterior margin acutely parabolic; face fairly flat. Pronotum rather cylindric, lateral margins impressed; mesonotum large, triangular; tegmina transparent; venation distinct; three ante-apical and four apical cells, inner apical cell rather large. Legs rather slender, hind tibiae elongate, twice as long as the femora.

**Dichrophleps despecta** Mel.

(Melichar, 1925a:330).

(Text-fig. 3 A-E).

I place the series of specimens in the present collection under this name because they resemble more closely the color markings described by Melichar for this species than they do the other species from British Guiana. Melichar describes the head as shorter than the pronotum, whereas in the present series the crown is longer than the pronotum.

The genital plates of the male when viewed ventrad are short, triangular, somewhat asymmetrical at the apex; the pygofers elongate, narrow, nearly as long as the anal segment, somewhat truncate at the apex, the whole surface set with short stout spines; the aedeagus elongate, stout, somewhat membraneous with a pair of ventral spines which are asymmetrical, the right spine being almost as long as the pygofer, the left spine shorter than the aedeagus; the apical area of the aedeagus is thin, irregularly broken into lobes. When viewed laterad the pygofer is about half again as long as its greatest width, thickly set with short, fairly stout spines.

Length to apex of tegmina: 16.3 mm.

Redescribed from 5 males from Kartabo, Bartica District, British Guiana. Dec. 5, 1920; April 4, 1924; April 6, 1924.

**Poeciloscarta** Stål, 1869a:73.

(*Cardioscarta* Melichar, 1932a:285).

Logotype *Tettigoniella* (*Poeciloscarta*) *cardinalis* Fabr.

Stål established this genus as a subgenus of *Tettigonia* as indicated above, for thirteen species from South America. Melichar established the new genus *Cardioscarta* for species from America and assigned Stål's genus to species from Madagascar and Africa. On what basis this was made has never been revealed as Melichar did not finish his work on this group.

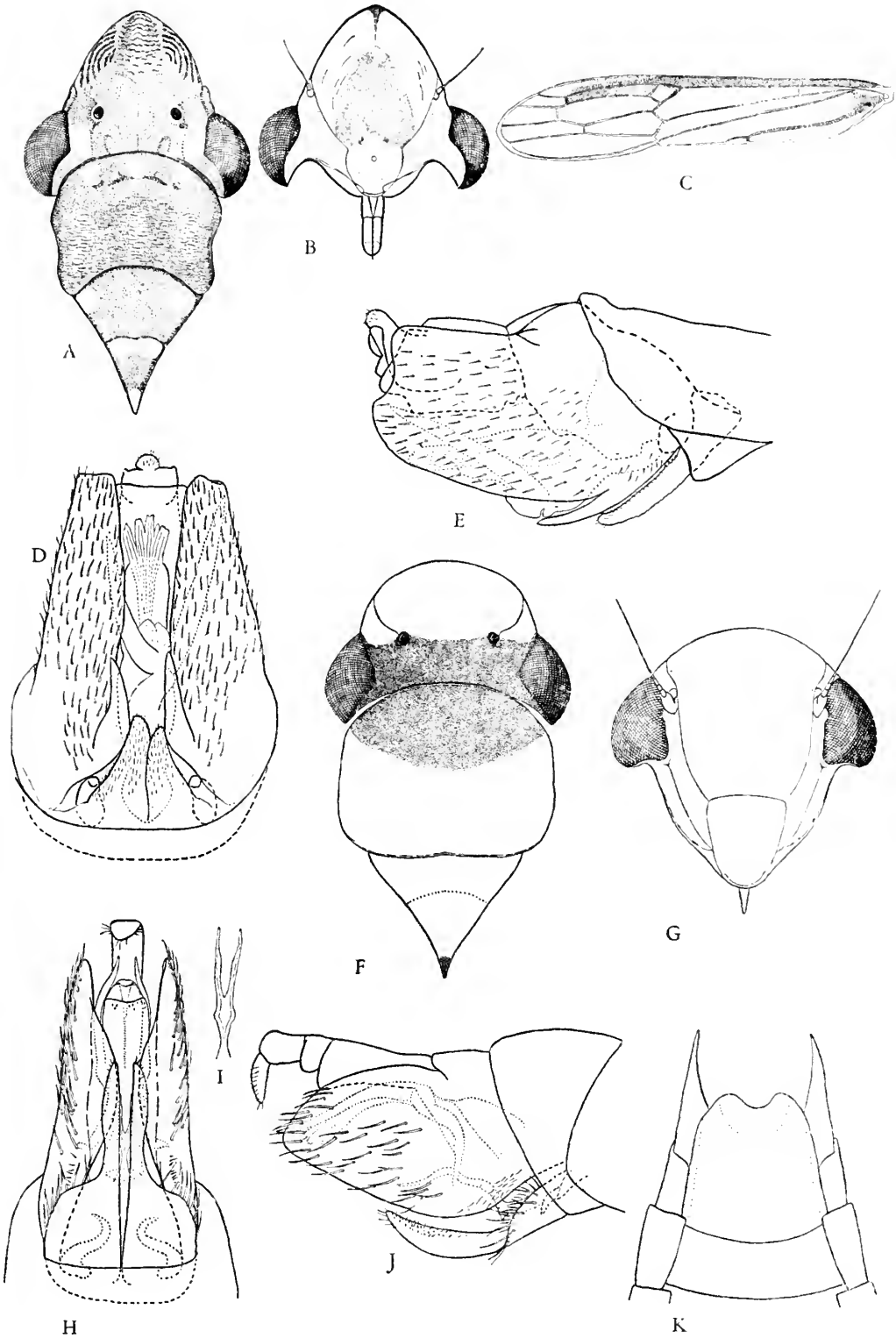
The genus may be defined briefly as follows: head including compound eyes broader than the pronotum; crown somewhat elongate, usually distinctly broader than long; anterior margin broadly parabolic; face elongate, not impressed. Pronotum broader than long, longer than the crown; anterior margin broadly curved; posterior margin nearly straight. Mesonotum large, shorter than the pronotum. Tegmina with the basal area of the corium and the clavus coriaceous with the venation indistinct; apex beyond the clavus translucent.

**Poeciloscarta quadrifasciata** Linnaeus.

(*Cardioscarta fasciata* Melichar, 1932a:300).

(Text-fig. 3 F-K).

There has been a great deal of confusion in the nomenclature of this species. It was described originally as *Cicada quadrifasciata* Linnaeus, 1767a:706. In this he was followed by the earlier subsequent writers who merely repeated his short but distinctive description and added the reference to the original description. Goeze, 1778a:130; Fabricius, 1781a:329, 1787a:274, 1794a:51 and 1803a: 72; de Tigny, 1802a:152; Donovan, 1820a: [6]; and Stoll, 1788a:82; pl. XXI, fig. 114A




TEXT-FIG. 3. *Dichrophleps despecta*: **A**, head thorax; **B**, face; **C**, tegmen; **D**, male genitalia ventral; **E**, male genitalia lateral. *Poeciloscarta quadrifasciata*: **F**, head thorax; **G**, face; **H**, male genitalia ventral; **I**, aedeagus ventral view; **J**, male genitalia lateral; **K**, female genitalia.

and 1792a:64; pl. XXI, fig. 114A described and illustrated this species as *fasciata* Linnaeus. In this they were followed by Blanchard, 1840a:190, and again in 1850a:190.

This species varies somewhat in color from light yellow to brilliant orange. Marked dorsad with four broad blackish fasciae, the first across the compound eyes, the posterior margin of the crown and the anterior margin of the pronotum; the second across the basal part of the tegmina beyond the sutural angle; the third across the apex of the clavus; and the fourth at the apex of the tegmina. The dark bands on the tegmina are quite variable in width and in color. The band at the apex of the tegmina is especially variable and is in some specimens reduced to a small fuscous spot with the apex of the tegmina translucent fuscous. The wings are translucent smoky with two blackish fuscous bands similar to the middle and the apical bands of the tegmina. The dorsal part of the abdomen is more or less marked with black; the venter and legs usually pale yellowish.

Crown broader than long, distinctly impressed in front of the compound eyes, broadly rounded to the face; the anterior margin parabolic; the posterior margin broadly sinuate. Pronotum quadrate; the anterior margin broadly rounded, the posterior margin nearly straight; face narrow, the anteclypeus large and protuberant.

Female genitalia with the last ventral segment elongate, nearly three times as long as the penultimate, the posterior border deeply and roundly emarginate; the male genitalia with the anal segment longer than the pygofers; the pygofers elongate, when viewed ventrad, broadened from the base to the middle and then constricted to the narrow apices; genital plates nearly as broad at the base as the last ventral segment, suddenly constricted at the middle and continued as a biramose process for half the length of the pygofers; the aedeagus elongate, stout with a biramose process, ventrally at the apex of the basal third, and a pair of elongate acute spines at the base of the apical third.

Length to apex of tegmina: 9.5 mm.

Described from numerous specimens from Kartabo, Bartica District, British Guiana.

Melichar distinguishes another species under the name of *Cardioscarta quadrifasciata* Fabr. under the assumption that *Cercopis quadrifasciata* Fabr. was a distinct species from Linnaeus's *Cicada quadrifasciata*. This cannot be true, however, as Fabricius, 1781a:329, merely copies Linnaeus's description and cites *Cicada quadrifasciata* as a synonym. Melichar distinguishes the two species in his key on the basis that *fasciata* Linnaeus (*quadrifasciata* Linnaeus) has two narrow bands on the tegmina, *quadrifasciata* Fabr. has three broad bands. This cannot be correct, however, as all of the descriptions and illustrations of the true *quadrifasciata* Linnaeus show three broad bands on the tegmina. As shown above *quadrifasciata* Fabr. is the same as *quadrifasciata* Linnaeus and I would synonymize *quadrifasciata* Melichar with *quadrifasciata* Linnaeus but for the fact that Melichar describes the male genitalia of the latter species as having the genital plates short; whereas in *fasciata*, that is, the true *quadrifasciata* Linnaeus, the genital plates are described as long. Until we can know more about these two species, it would seem best to give a new name to Melichar's *quadrifasciata* Fabr. and I propose **Poeciloscarta nigrofasciata** nom. nov. for *Cardioscarta quadrifasciata* Melichar nec *Cercopis quadrifasciata* Fabr. This species should not be confused with *Tettigonia fabricii* which Signoret proposed for *Fulgora fasciata* Fabr. under the assumption that *fasciata* Fabr. was a secondary homonym of *Cicada fasciata* [sic] Linnaeus. But since *fasciata* Linnaeus is a typographical error for *quadrifasciata* Linnaeus and belongs to the genus *Poeciloscarta*, and *fasciata* Fabr. belongs to the genus *Raphirhinus*, the correct synonymy for Fabricius' species is as follows:

*Raphirhinus fasciatus* Fabr.

*Fulgora flammea* [nec Linnaeus] Stoll, 1781a:28; pl. VI, fig. 29.

*Fulgora fasciata* Fabricius, 1787a:261.

*Raphirhinus obliquatus* de Laporte, 1832d: 415.

*Tettigonia fabricii* Signoret, 1855c:521; pl. 21, fig. 12.

**Raphirhinus** de Laporte, 1832d:413.

Orthotype *Fulgora abscendens* Fabr.
i.e., *Fulgora phosphorea* Linnaeus.

This is one of the most distinct genera of the subfamily Proconinae. It may be characterized briefly as follows:

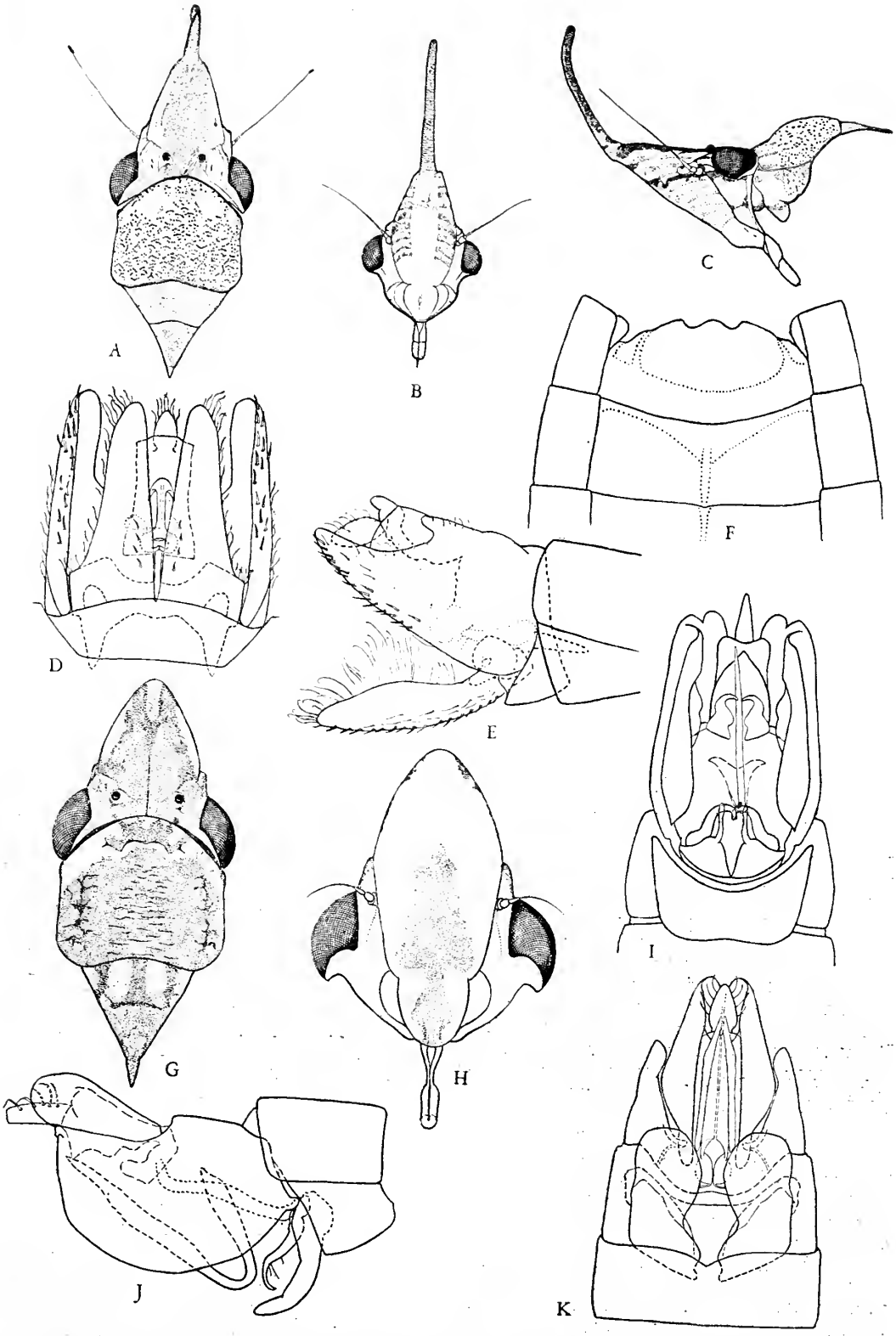
Head including compound eyes as wide as the pronotum suddenly constricted in front of compound eyes, triangularly produced to the obtuse apex which is continued into an elongate, terete, erect, somewhat recurved slender process. Pronotum usually slightly broader than long; lateral margin slightly divergent; anterior margin broadly curved, the posterior margin triangularly incised, sinuate. Mesonotum nearly as long as the pronotum, triangular. Legs slender; the anterior tibiae broadly expanded apically. Tegmina elongate, slender, coriaceous; venation fairly distinct.

**Raphirhinus phosphoreus** Linnaeus.

(Melichar, 1925a:354).

(Text-fig. 4 A-F).

This species is very variable in color. The females are chiefly ferruginous, heavily speckled with light yellow dots dorsad. Ventrad chiefly ochraceous. Males chiefly blackish fuscous, dorsad with the median area of cephalic process, lateral margins of crown, and pronotum yellowish testaceous. Beneath chiefly light testaceous yellow with postclypeus pro- and meso- plura twice banded




TEXT-FIG. 4. *Raphirhinus phosphoreus*: **A**, head thorax; **B**, face; **C**, lateral head thorax; **D**, male genitalia ventral; **E**, male genitalia lateral; **F**, female genitalia. *Capinota virescens*; **G**, head thorax; **H**, face; **I**, male genitalia ventral; **J**, male genitalia lateral; **K**, female genitalia.

with blackish fuscous; the fore tibiae and middle tarsi and hind tarsi apically blackish fuscous.

Female last ventral segment slightly longer than preceding segment; the apical margin on the median third shallowly bisinuate with a broad obtuse tooth. Male genitalia with pygofers, genital plates and anal segments all approximately the same length. The genital plates elongate, somewhat triangular, obtuse at the apex. The aedeagus capitate with the lateral margins strongly produced.

Length to apex of tegmina: 13.7-18.5 mm.

British Guiana, French Guiana and Surinam. Kartabo, Bartica District.

**Raphirhinus fasciatus** Fabr.

(*Fulgora fasciatus* Fabricius, 1787a: 261).

This common and well-known species has been recorded previously from Surinam, French Guiana, Peru, Bolivia and in Brazil from Amazonas, Para and Bahia. It may be recognized by its large size and its characteristic color and markings. The dorsal surface is chiefly testaceous brown with a central vitta on the cephalic process, lateral margins of the crown, most of the pronotum, the basal area of the tegmina, a narrow fascia beyond the apex of the mesonotum, a broader fascia covering the apex of the clavus and an irregular fascia just before the apical cells, grayish or greenish-yellow. Beneath, the color is pale yellow with two narrow brownish vittae extending across the face, the lateral margins of the head, the pro- and meso-pleura to the base of the tegmina. The dorsal vitta extends just below the compound eyes and the lateral margins of the pronotum; the ventral vitta just above the clypeal suture and then curved upward to the base of the tegmina. The tips of all the tarsi and tibiae blackish fuscous.

The female last ventral segment is longer than the penultimate with the lateral margins broadly sinuate; the median area broadly and shallowly sinuate, with a broad obtuse tooth on the median line.

**Capinota** Melichar, 1926a:319.

Orthotype *Capinota fowleri* Mel.

This genus was described originally for a single species from Mexico. The present collection contains a single species which I assigned to this genus with some hesitation, but apparently the present species should be included here.

Head including compound eyes broader than pronotum. Crown elongate, produced, suddenly but not strongly constricted in front of the compound eyes. Apex broadly upturned, impressed on the median line; lateral margins of the impression slightly carinate; a fine median carina from the base to the indented apex. Ocelli behind the anterior margin of the compound eyes. Face strongly inflated. Anteclypeus rather large, strongly inflated. Pronotum slightly broader than long; anterior margin broadly rounded; lateral margins nearly parallel; posterior margin slightly indented. Mesonotum large, nearly as long as the pronotum. Legs slender; anterior tibiae not grooved; posterior tibiae elongate, about twice as long as the femora; basitarsus elongate, longer than the other two segments combined. Tegmina narrow; costal and commisural margins nearly parallel, coriaceous; venation regular but not very distinct: claval veins parallel.

**Capinota virescens** n. sp.

(Text-fig. 4 G-K).

This species may be recognized by its general fuscous color above with a decided greenish cast; beneath chiefly ochraceous yellow with the tibiae of the legs chiefly ochraceous orange; ventral portion of the postclypeus clouded with blackish; anteclypeus chiefly blackish fuscous on the median line. Crown nearly one and one-half times as long as the width betwen the compound eyes. Ocelli nearly three times as far from each other as from the compound eyes. Pronotum slightly broader than long; sides nearly parallel; the whole surface finely but irregularly rugulose.

Male genitalia with the genital plate broadly triangular at the base, deeply incised on the median line. Inner caudal angles produced into two elongate, slender processes. Genital styles elongate, slender, curving inward, hooked at the apex. Pygofers large with a distinct ridge on the inner ventral margin. Aedeagal strut elongate, slender, acuminate and recurved at the apex. Aedeagus elongate, needle-like, sharply elbowed on basal third; basal area broadly Y-shaped when viewed ventrad. Anal segments elongate, terete, with a pair of ventral hooks at the base. Anal style elongate, slender, somewhat sagittate with a pair of distinct leaf-like processes arising at the base of the anal segment and covering most of the anal segment and anal style laterad and dorsad.

General color of the male above fuscous with a greenish cast; lateral margins of the crown, anterior border of the pronotum, and costal margin of the male greenish-yellow. Beneath ochraceous yellow except the conspicuous blackish cloud on the anteclypeus and postclypeus and the ochraceous orange tibiae and tarsi. Dorsum of the abdomen blackish fuscous; lateral margins ochraceous yellow; tips of tegmina translucent.

Length to apex of tegmina: 10.52 mm.

Holotype ♂: British Guiana without definite date or locality.

Allotype ♀: Kartabo, Bartica District, British Guiana, September 20, 1922.

Paratypes: 1 ♂: Kartabo, Bartica District, British Guiana, August 13, 1920; 1 ♀: British Guiana without definite date or locality.

**Rhopalogonia** Mel.

(Melichar, 1926a:341).

Logotype *Rhopalogonia scita* Walk.

Head broad, including compound eyes

broader than pronotum; crown much broader than long, broadly rounded to face. Ocelli placed near the posterior border of the crown and near the compound eyes. Pronotum broad, nearly twice as broad as the median length. Mesonotum broad, not as long as the pronotum. Tegmina coriaceous, elongate, narrow; apical margin broadly rounded; venation indistinct, regular with four apical and three ante-apical cells, claval veins nearly parallel, complete. Legs elongate, slender; all tibiae more or less quadrangular; fore tibiae slightly longer than femora, middle tibiae more elongate and hind tibiae nearly twice as long as the femora.

**Rhopalogonia purpurata** Germ.

(*Tettigonia purpurata* Germar, 1821a:63).
(*Tettigonia purpurata* Signoret, 1853b:325, Pl. 8, Fig. 2).
(*Tetigonia purpurata* Osborn, 1926b:200).
(Text-fig. 5 A-E).

There is a small series in the present collection which I believe represents this species as described by Germar and described and illustrated by Signoret, despite the differences in coloration.

Head short and broad, crown nearly three times as broad as the median length, distinctly bi-impressed. Impressions including the large ocelli connected by a broad transverse groove; posterior border broadly carinate; anterior border broadly curved; posterior margin nearly straight. Face inflated, the postclypeus distinctly angulate near the middle. Pronotum about half again as broad as the median length, anterior margin broadly rounded, posterior margin nearly straight; mesonotum large, broader than long.

Female last ventral segment longer than broad, more than three times as long as the penultimate with a broad triangular median tooth and a pair of small lateral triangular teeth at the apex. Male genitalia with the genital plates, anal segment and pygofers all about the same length. Genital plates elongate, slender, obtuse at the apex; pygofers elongate, slender, very obtuse at the apex; aedeagus about half as long as the genital plates, broadened into two distinct lobes apically, with the outer posterior angle broadly produced; genital styles elongate, slender, curving outward; apices reflexed.

General color chestnut brown, usually distinctly lighter on the head, with a distinct round spot at the apex of the crown, blackish fuscous. Pronotum chiefly chestnut brown with a broad fascia across the middle, grayish-white. Tegmina crossed by two bluish-white fascia, one immediately posterior to the apex of mesonotum and the other near the apex of the clavus. Venter including legs chiefly chestnut brown.

Length to apex of tegmina: 11.0-11.5 mm.

Redescribed from a series of four specimens, two from Georgetown, British Guiana, and two from Bartica District, British Guiana. This species has previously been recorded from Surinam, French Guiana, and various localities in Brazil.

## Family Gyponidae.

In this family the body is elongate, depressed. The head is usually broad but narrower than the pronotum at the posterior lateral angles. The crown is usually longer than broad with the ocelli on the disc. The anterior margin of the crown is thin and foliaceous, or broadly thickened or rounded to the face. The face is usually broad, usually suddenly widened at the level of the antennae and forming a distinct antennal ledge. The postclypeus is narrow and elongate. The lora conspicuous. The genae broad and flat. The pronotum is large with the anterior lateral margins rounding into the anterior margin with the anterior lateral angles inconspicuous. Posterior lateral angles usually conspicuous. The posterior lateral margins distinct. The posterior margin usually broadly incised. Mesonotum large, nearly as broad as long. Anterior and intermediate femora and tibiae with distinct spines. Posterior tibiae with the internal and external dorsal margins and the external ventral margin with several fairly close set heavy spines; the internal ventral margins fringed with numerous more or less hair-like spines. Tegmina coriaceous or translucent; venation distinct, sometimes reticulate over the whole surface or the apical third only; radius 2 branched; media unbranched; cubitus 1 with two branches; cubitus 2 unbranched; first and second anal veins distinct. There are typically a single cross vein between the radial sectors; two radio-medial cross veins; and two medio-cubital cross veins thus forming three ante-apical and four apical cells.

### Key to Genera of Gyponidae.

A. Head with a cephalic process.
*Ohausia* Schmidt, 1911b:299

AA. Head without a cephalic process.

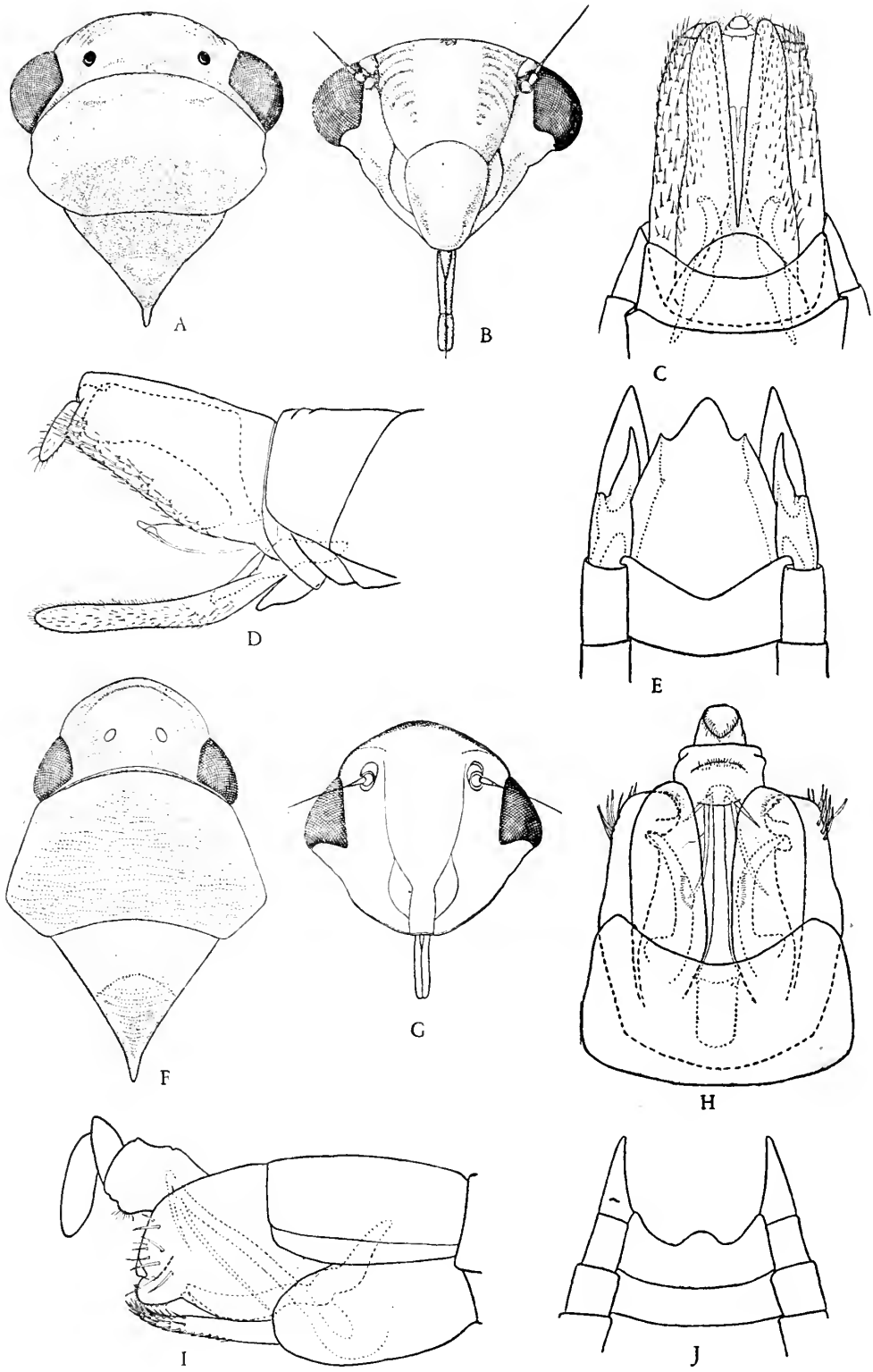
B. Tegmina uniformly deeply pitted, body dorsoventrally wedge-shaped anteriorly, transversely wedge-shaped posteriorly, tegmina vertical, laterally compressed at apex.
*Dragonana* Ball and Reeves, 1927a:489

BB. Tegmina not pitted except along veins, tegmina not appressed at apex.

C. Tegmina with numerous reticulate veins, at least on apical portion.

1. Tegmina rugose or roughened, often with white mottling, crown and pronotum usually rugose, two round black spots on pronotum.
*Rugosana* DeLong, 1942a:64

1. Tegmina with venation often prominent but not rugose or




TEXT-FIG. 5. *Rhopalogonia purpurata*: **A**, head thorax; **B**, face; **C**, male genitalia ventral; **D**, male genitalia lateral; **E**, female genitalia. *Gypona thoracica*: **F**, head thorax; **G**, face; **H**, male genitalia ventral; **I**, male genitalia lateral. *Gypona bigemmis*: **J**, female genitalia.

roughened, crown and pronotum never rugose.
*Gyponana* Ball, 1920a:85

CC. Tegmina without reticulate veins, typically with four apical and three subapical cells.

1. Face narrow, deeply excavate; pronotum and tegmina coarsely rugose.
*Rhogosana* Osborn, 1938a:14

1. Face not deeply excavated, flat or inflated ..... 2

2. Crown acutely angled with front, margin thin, sharp, or foliaceous ..... 3

2. Crown with thick margin or broadly rounding to front 6

3. Crown flat with longitudinal furrows, ocelli on furrow each side of median line. Tegmina usually marked with brownish dots or lines in areoles.
*Prairiana* Ball, 1920a:90

3. Crown without longitudinal furrows, tegmina usually without brownish markings in areoles, or if present without small brown punctate spots on vertex ..... 4

4. Body usually dorsoventrally thickened, pronotum and crown depressed anteriorly, strongly sloping to anterior foliaceous margin ..... 5

4. Body usually dorsoventrally flattened, pronotum and crown almost flat or gently sloping to foliaceous margin.
*Acusana* DeLong, 1942d :57

5. Color black, green, or orange-yellow; crown with narrow longitudinal stripes, or two round black spots on pronotum, or both.
Male styles short, blunt, or truncate at apex.
*Gypona* Germar, 1821a:73

5. Color green or brown, without stripes on crown or round black spots on pronotum. Male styles long, slender, apex with curved, pointed tips.
*Hamana* DeLong, 1942d:85

6. Crown with distinct thick margin ..... 7

6. Crown without definite margin, broadly and evenly rounded to front as viewed laterad ..... 11

7. Face strongly inflated or bulbous ..... 8

7. Face not inflated, almost straight in profile, color some shade of yellow or brown usually with distinct dark markings ..... 9

8. Crown elongate, ocelli near anterior margin. Mesonotum not longer than pronotum.
*Bulbana* DeLong, 1942d:107

8. Crown short and broad. Ocelli about equi-distant from anterior and posterior margins. Mesonotum longer than the pronotum.
*Scaris* LeP. and Serv.

9. Pronotum conspicuously wider than crown, ocelli large, located almost half the length of crown from anterior border.
*Ponana* Ball, 1920a:93

9. Pronotum scarcely wider than crown, ocelli anterior to middle in the depression above margin ..... 10

10. Anterior margin of crown quadricarinate.
*Marganalana* Metcalf

10. Anterior margin of crown not quadricarinate.
*Marganana* DeLong, 1948b:101
[*Margana* DeLong, 1942d:109]

11. Ocelli on anterior border of crown.
*Polana* DeLong, 1942d:110

11. Ocelli on disc ..... 12

12. Head including compound eyes nearly as broad as pronotum.
*Scaroidana* Osborn, 1938a:49

12. Head including compound eyes decidedly narrower than pronotum ..... 13

13. Crown short and broad, usually more than three times as broad as its median length ..... 14

13. Crown and pronotum longer, usually not more than twice as broad as their median lengths.
*Scarisana* Metcalf

14. Pronotum short and broad, more than three times as broad as median length; humeri prominent; the anterior lateral and posterior lateral margins about the same length.
*Clinonana* Osborn, 1938a:13

14. Pronotum not more than twice as broad as long; humeri not prominent; anterior lateral margins longer than the posterior lateral margins.
*Clinonaria* Metcalf

**Gypona** Germar, 1821a:73.

Haplotype *Cercopis glauca* Fabr.

This is a large genus of about 153 species, widely distributed from Canada, the United States, to Mexico, Central and South America as far south as Argentina and Chile. The genus formerly contained many species which are now distributed in other genera of the family Gyponidae. Many species now included in the genus *Gypona* undoubtedly belong to other genera which have been proposed recently. The correct disposition of many of the species described by Spangberg and earlier students has not been determined.

There are in the present small collection no less than 10 species of which 8 seem to be new. The genus may be described briefly as follows: body usually dorsoventrally thickened; pronotum and vertex depressed anteriorly, strongly sloping from the posterior margin of the pronotum to the anterior foliaceous margin of the crown which may be slightly upturned. Head narrower than the pronotum; crown usually elongate, sometimes almost as long as the width between the eyes. Ocelli variously placed on the crown; the anterior margin of the crown thin and foliaceous; face flat. Pronotum usually large with the anterior margin about as wide as the greatest width of the eyes; lateral margins strongly divergent, usually distinctly carinate; anterior and posterior margins strongly curved; mesonotum large; venation of the tegmina simple, the veins not punctate, with three ante-apical and four apical cells. Anterior and intermediate legs slender, short; posterior tibiae elongate with stout, close-set spines on the lateral and ventral borders. Male styles usually short and blunt at the apex. In color the species are usually decidedly variable with considerable sexual dimorphism. The females are usually light green or orange yellow, frequently unmarked, sometimes with narrow vittae on the crown or two black spots on the anterior border of the pronotum or both. Males are frequently black above, with or without pale vittae.

**Gypona fusiformis** Walker, 1858b:257.

There is a single female specimen in the present collection which agrees with Walker's short description. It may be described briefly as follows: head distinctly narrower than the pronotum; crown elongate, more than half as long as the pronotum; the anterior margins nearly parallel for a short distance in front of the compound eyes, then broadly and obtusely angulate. Ocelli behind the middle about as far from each other as from the compound eyes. Pronotum large, the lateral margins strongly divergent, anterior margin broadly rounded. Mesonotum large.

Tegmina translucent with the median apical cell clouded with blackish fuscous. Head, pronotum and mesonotum ochraceous tawny, the anterior margin of the crown narrowly blackish, veins of the tegmina, except the concolorous subcostal vein, blackish fuscous; wings translucent, the narrow apical margin blackish fuscous; beneath, ochraceous yellow, the claws of the anterior and middle legs blackish; tips of posterior tibiae and the tarsi blackish.

Female last ventral segment slightly longer on the median line than the penultimate. Lateral posterior angles broadly rounded; the posterior margin broadly, triangularly incised for nearly half the length of the segment.

Length to apex of tegmina: 14.5 mm.

**Gypona thoracica** Fabr.

(Osborn, 1938a:21).

(Text-fig. 5 F-I).

This species was described from South America without definite locality and has been recorded from various states in Brazil. There is a good series in the present collection from Bartica District, British Guiana, collected from March through May but none later in the year.

All specimens in the present collection are males. Most of them are black in color, dorsad, with a narrow longitudinal median vitta from the apex of the crown to the apex of the mesonontum. One specimen has the posterior half of the pronotum bright orange yellow; another specimen has the entire pronotum and mesonotum bright orange yellow, with the crown with a narrow median vitta and two large pale comma-shaped marks curving between the ocelli and the compound eyes. Beneath, all the specimens are pale yellow with the posterior tibiae and tarsi and the anterior margins of the segments black.

Crown elongate, more than half as long as the pronotum, about two-thirds as long as the greatest width between the eyes. Ocelli behind the middle about as far from each other as from the compound eyes. The anterior margin of crown broadly parabolic, slightly concave. Pronotum nearly twice as broad as median length, the anterior margin broadly curved, the posterior margin broadly sinuate.

Male genitalia with the pygofers and genital plates about the same length, shorter than the anal segment. The genital plates with parallel sides, obtuse at the apex. Pygofers when viewed laterad about as long as broad with a distinct ventral apical lobe. Genital styles elongate, acuminate and diverging cauded. Aedeagus elongate, slender with two pairs of spines at the apex, the ventral pair short, strongly divergent, the apical pair elongate, slightly divergent at the apex, about half as long as the aedeagus.

Length to apex of tegmina: 13.8-14.5 mm.

**Gypona bigemmis** Spangb.

(Osborn, 1938a:25)

(Text-fig. 5 J).

This species has been reported previously

from Rio de Janeiro, Colombia and Guatemala. It may be recognized by its small size, uniform pale greenish color, and distinctive female genitalia. Head broad and short; crown broadly rounded before, slightly more than twice as broad as the median length; ocelli slightly before the middle as remote from each other as from the compound eyes. Pronotum more than twice as long as the crown, more than twice as broad as its median length. Female last ventral segment slightly longer than the penultimate, deeply excavated with a broad, round median lobe.

Length to apex of tegmina: 6.5-7.5 mm.

There is a single female in the present collection from Kartabo, Bartica District, British Guiana, March 6, 1924.

### *Gypona flavolimbata* n. sp.

(Text-fig. 6 A-E).

This is a medium large species closely resembling *Gypona glauca* Fabr. in general coloration but differing decidedly in female genitalia.

Head broad, only slightly narrower than the pronotum; crown twice as broad as its median length; ocelli just behind the middle as far from each other as from the compound eyes. Pronotum twice as broad as its median length; anterior margin broadly rounded; anterior lateral margins nearly straight, slightly divergent; posterior margin shallowly rounded almost parallel to the anterior margin. Mesonotum large.

Female with the last ventral segment only slightly longer on the median line than the penultimate; the posterior margin shallowly incised with a broad median tooth with a small triangular notch at the apex; the posterior lateral angles only slightly produced. Male genitalia when viewed ventrad with the pygofer narrow, distinctly appendiculate. Genital plates shorter than the pygofer with the apex obtuse; genital styles elongate, acute at the apex, as long as the pygofer; aedeagus as long as the pygofer, the apex with two elongate slender spines. The pygofer when viewed laterad about as broad as long with the posterior dorsal angle distinctly produced.

Length ♂: 9.75 mm.-10 mm. Length ♀: 10.75-11 mm.

Holotype ♂: British Guiana without definite date or locality.

Allotype ♀: Kartabo, Bartica District, British Guiana, March 25, 1922.

Paratypes 1 ♂: British Guiana without definite date or locality; 1 ♀: Kartabo, Bartica District, British Guiana.

### *Gypona translucens* n. sp.

(Text-fig. 7 A-C).

This species resembles *Gypona fusiformis* Walk. very closely. Head narrow, broadly triangularly produced, the crown more than half as long as the pronotum. The ocelli behind the middle, about as far from each other as from the compound eyes. Pronotum large, the lateral margins strongly divergent, the whole surface coarsely rugulose; tegmina semitransparent.

Female last ventral segment about as long on the median line as the penultimate segment; lateral posterior angles strongly produced, the posterior margin broadly, parabolically incised with the incision slightly produced either side of the median line in short, blunt lobes.

General color tawny; the tegmina translucent; the anterior border of the crown narrowly blackish; the veins of the tegmina blackish fuscous except subcosta, which is chiefly yellowish-brown; beneath, including the legs, pale ochraceous yellow; the claws and some of the spines blackish fuscous.

Length to apex of tegmina: 17.0 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, August 18, 1920.

Paratype ♀: Kartabo, Bartica District, British Guiana, August 9, 1920.

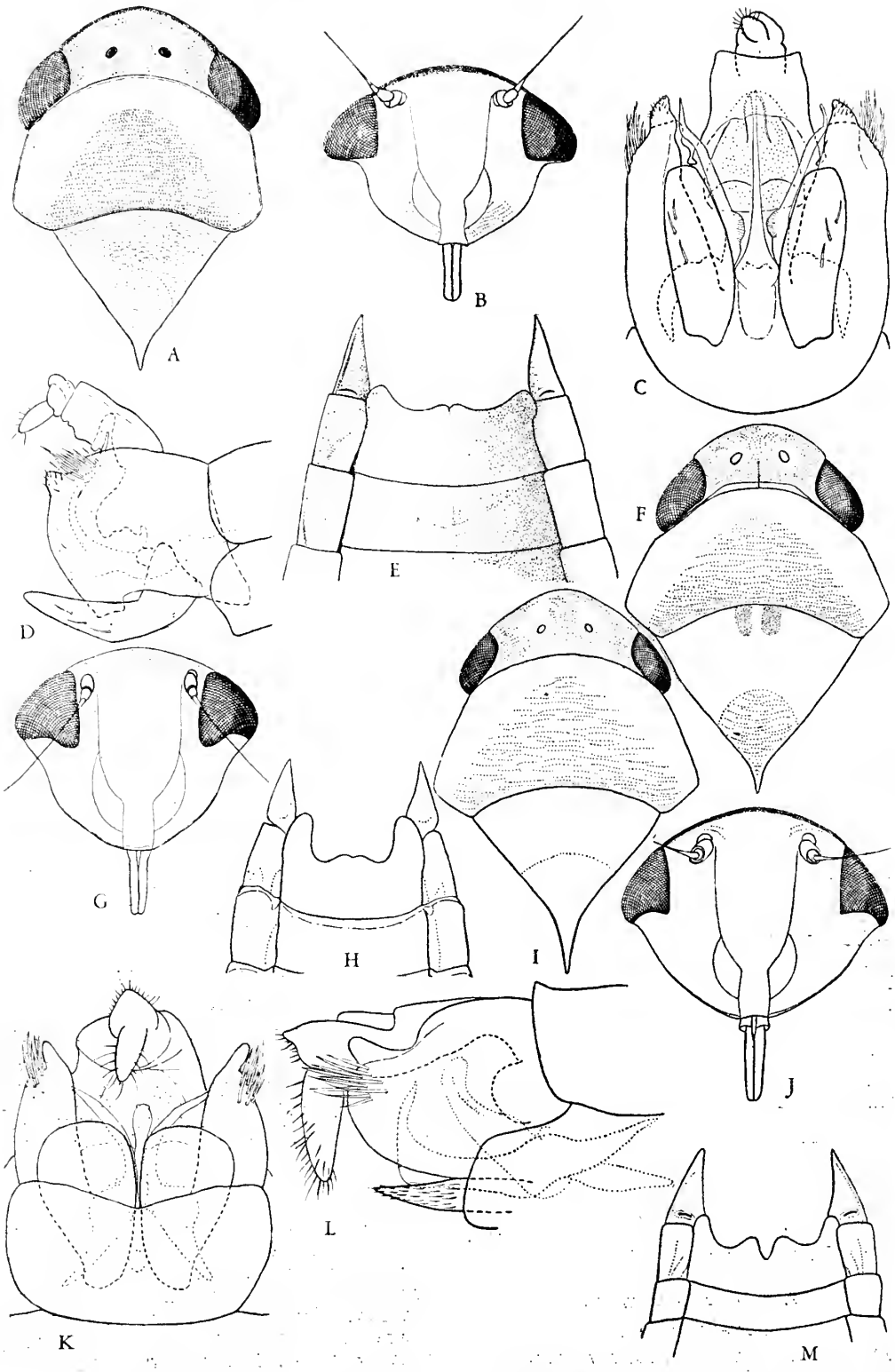
### *Gypona picturata* n. sp.

(Text-fig. 6 I-M).

This is one of the most conspicuously colored Gyponas known to me. In general structure it resembles somewhat *Gypona peruviana* Osb. but differs in essential details of the female genitalia and decidedly in coloration. Head narrow, crown short and median length about one-half as long as the greatest width between the eyes. Pronotum short and broad, about twice as long as the crown, its median length about one-half its greatest width; the anterior margin broadly curved, anterior lateral borders carinate, about twice as long as the posterior lateral margins; posterior margin nearly parallel to the anterior margin. Tegmina short and broad; venation regular.

Female last ventral segment nearly twice as long as the penultimate; the lateral posterior angle strongly produced, broadly rounded. Median area strongly produced with a deep notch on the median line. Male genitalia with genital plates short and broad, broadly rounded at apex; pygofers shorter than anal segment distinctly appendiculate; genital styles slender, elongate, strongly diverging caudad; aedeagus elongate, somewhat bulbous with a distinct process apically directed dorsad.

General color above, pale greenish-yellow with the crown with a bright red anterior border and a pair of pale reddish vittae through the ocelli; the pronotum with three pairs of reddish vittae; the tegmina chiefly translucent greenish-yellow, more or less clouded with brownish and blackish; the clavus is chiefly brownish with a broad saddle of white just before the apex; the claval border and the sutural border and the veins chiefly blackish; some of the veins on the corium are blackish or brownish and the apex is narrowly bordered with blackish fuscous with a cloud of blackish or brownish fuscous across the apical cross-veins. Be-




TEXT-FIG. 6. *Gypona flavolimbata*: **A**, head thorax; **B**, face; **C**, male genitalia ventral; **D**, male genitalia lateral; **E**, female genitalia. *Gypona castanea*: **F**, head thorax; **G**, face; **H**, female genitalia. *Gypona picturata*: **I**, head thorax; **J**, face; **K**, male genitalia ventral; **L**, male genitalia lateral; **M**, female genitalia.

neath, pale ochraceous yellow with all the tibiae and tarsi brownish fuscous.

Length ♀ to apex of tegmina: 13.5 mm.; ♂: 11.5 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, March 17, 1922.

Allotype ♂: Georgetown, November 15, 1933.

Paratype ♀: Kartabo, Bartica District, British Guiana, March 17, 1922.

### **Gypona opaca** n. sp.

This is another large species somewhat similar in coloration to *Gypona fusiformis* Walk. and *Gypona translucens* Metc. in that the head and pronotum are generally lighter than the tegmina. It differs, however, in that the crown is very much shorter, the tegmina are opaque and variegated, and the anterior margin of the crown is without the narrow black border.

Head narrow; crown broad and short, about half as long as the short pronotum; the anterior margin broadly parabolic; the ocelli slightly behind the middle, about as far from each other as from the compound eyes; the anterior margin thin and foliaceous. Pronotum short and broad, nearly twice as broad as the median length; the lateral margins short, strongly carinate, slightly divergent; the posterior lateral margins about half as long as the anterior lateral margins; anterior margin broadly curved with posterior border nearly parallel. Tegmina opaque, somewhat rugulose. Face very flat; the dorsal margin distinctly impressed with a nearly quadrate impressed point.

Female last ventral segment somewhat longer than the penultimate on the median line. The lateral posterior angles broadly produced, somewhat obtuse. The posterior margin broadly, roundly incised either side of a strongly produced, rounded tooth.

General color of the head and thorax above, yellowish-tawny; the ocelli and compound eyes black; tegmina generally reddish-brown, variegated with pale yellowish over most of the surface; the costal margin with the reddish-brown and yellowish spots rather regularly distributed. The whole area of the tegmina somewhat rugulose but the venation regular. General color beneath, yellowish-tawny with the dorsal margin of the face infuscated; legs chiefly reddish-brown with the spines of the hind tibiae blackish fuscous.

Length to apex of tegmina: 15 mm.

Holotype ♀: Kartabo, Bartica District, British Guiana, April 4, 1922.

### **Gypona castanea** n. sp.

(Text-fig. 6 F-H).

This is an almost uniformly castaneous brown species of fairly large size with the venter of the abdomen a little paler and two conspicuous black spots on the anterior border of the mesonotum.

Head narrower than the pronotum; the crown about twice as broad as its median length; the ocelli almost equidistant from each other and the eyes, placed near the middle of crown; the anterior margin strongly curved. Pronotum twice as long as the crown, more than twice as broad as its median length; anterior margin broadly curved; anterior lateral margins nearly straight, not quite twice as long as the posterior lateral margins; posterior margin deeply incised; surface of pronotum strongly rugulose.

Last ventral segment of the female longer than the penultimate, deeply, almost quadrately incised with a broad median tooth which is notched at the apex; posterior lateral angles strongly produced, distinctly rounded at the apex.

Color almost uniformly castaneous above and beneath, except the basal segments of the abdomen which are slightly paler. Mesonotum with two conspicuous black spots on the anterior border. Tegmina with a row of inconspicuous brownish-yellow spots in the costal cell and a few irregular scattered spots on the corium and the clavus; apex of the tegmina infuscate.

Length to apex of tegmina: 11.7 mm.

Holotype ♀: British Guiana without definite date.

### **Ponana** Ball.

*Gypona* (*Ponana*) Ball, 1920a:93.

Orthotype *Gypona scarlatina* Fitch.

This genus may be recognized by its narrow head, narrower than the posterior angles of the pronotum, crown short with a distinct thick margin separating it from the face. Face flat, distinctly impressed beneath the broad border. Mesonotum large. Tegmina coriaceous, venation regular. Pronotum broad; anterior margin broadly curved, almost continuous with anterior lateral margin; posterior margin nearly straight. Whole surface finely rugulose.

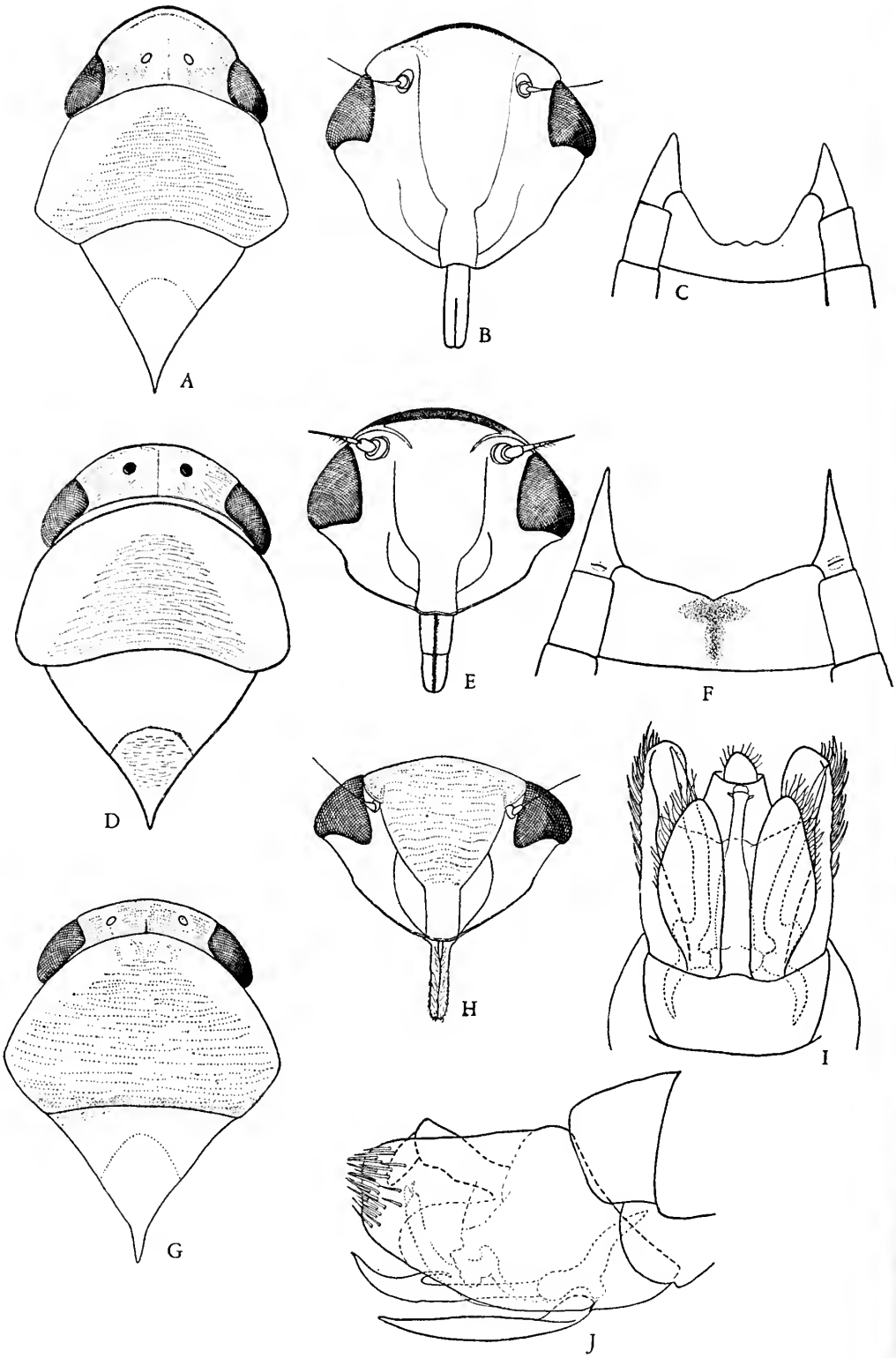
### **Ponana fulva** n. sp.

(Text-fig. 7 D-F).

This is an almost uniformly tawny-colored species with the thick anterior margin brown, the ocelli and compound eyes black. Dorsal margin of abdomen chiefly bright carmine red. Crown broad and short, nearly two and a half times as broad as its median length; anterior margin broadly thickened. Ocelli about as far from base as from apex, almost equidistant from each other and the compound eyes. Face distinctly impressed beneath a broad dorsal margin. Pronotum not quite twice as broad as its median length; anterior lateral margins not distinctly separated from anterior margin; posterior lateral margins short; posterior margin broadly incised. Mesonotum nearly as broad as the head, broader than long.

Female last ventral segment about as long as penultimate; posterior margin broadly V-shaped; posterior lateral angles not produced.

Length to apex of tegmina: 9.50 mm.




TEXT-FIG. 7. *Gypona translucens*: **A**, head thorax; **B**, face; **C**, female genitalia. *Ponana fulva*: **D**, head thorax; **E**, face; **F**, female genitalia. *Clinonaria bicolor*: **G**, head thorax; **H**, face; **I**, male genitalia ventral; **J**, male genitalia lateral.

Holotype ♀: British Guiana without definite date or locality.

**Clinonaria** gen. n.

Orthotype *Clinonaria bicolor* n. sp.

This genus may be recognized by its narrow head with short broad crown. The pronotum is not especially broad and the humeri are not very prominent. When viewed laterad the pronotum is strongly declivous and the crown is broadly rounded to the face. Tegmina somewhat rugulose but the venation is distinct.

**Clinonaria bicolor** n. sp.

(Text-fig. 7 G-J).

This species resembles *Clinonana declivata* Osb. but differs in detail and decidedly in color. Head narrow; crown very short and broad with the ocelli near the anterior margin. Anterior margin broadly rounded to the face. Pronotum short, not very broad; mesonotum large.

Male genitalia with the pygofers rather broad, obtuse at the apex. Genital plates shorter than pygofers, narrow at the base, broadly curved on the lateral margins; apices obtuse; genital styles elongate, as long as the pygofers with an obtuse basal expansion; aedeagus large on the basal half, gradually narrow to the apical third with two short spines at the apex.

General color of the crown and pronotum ochraceous orange; compound eyes and ocelli black; narrow posterior border of the pronotum brown, margined anteriorly with pale green; mesonotum and tegmina auburn brown; tegmina with irregular blackish fuscous spots along the costal margin and on the basal and apical thirds; face chiefly ochraceous orange. General color beneath yellowish ochraceous with the apex of the fore, middle and hind femora with a large blackish spot near the apex; spines on the middle and hind tibiae with large black spots at their bases; apex of the hind tibiae black.

Length to apex of tegmina: ♂ 11.75 mm.; ♀ 13.0 mm.

Allotype ♀: British Guiana without definite locality or date.

Holotype ♂: Kartabo, Bartica District, British Guiana, July 20, 1922.

**Marganalana** n. gen.

Orthotype *Marganalana testacea* n. sp.

This genus is close to *Marganana* DeLong (*Margana* DeLong) but differs in several respects. Head narrower than the pronotum; crown twice as broad as long; anterior margin parabolic; ocelli nearly equidistant from the anterior and posterior margin. Anterior margin of the head conspicuously thickened, quinquecarinate, not distinctly impressed above or below. Face flat, narrow; pronotum slightly more than twice as long as the crown, not quite twice as broad as long; anterior lateral margins elongate; posterior lateral margins short; anterior margin broadly curved in an almost continuous line from the humeri; posterior margin nearly straight. Mesonontum large. Tegmina with the venation regular. The main veins of the corium and clavus with a few indistinct punctures.

**Marganalana testacea** n. sp.

(Tex-fig. 8 A-D).

Crown distinctly broader than long; anterior margin broadly curved; median length greater than length next to compound eyes. Ocelli conspicuous, about as far from each other as from the compound eyes. Pronotum not twice as broad as long, scarcely longer than mesonotum. Female last ventral segment nearly twice as long as the penultimate with a broad V-shaped shallow notch on the posterior border; posterior lateral angles not produced.

General color above and below tawny, with anterior margin of crown, compound eyes and ocelli black. The apex of the tegmina infuscate. Dorsal segments of the abdomen chiefly scarlet red.

Length to apex of tegmina: 8.5 mm.

Holotype ♀: British Guiana without definite date or locality.

**Scarisana** n. gen.

Orthotype *Scarisana variabilis* n. sp.

This genus may be recognized by the long broad head which is nearly as broad as the pronotum. Crown long and broad; anterior margin broadly parabolic; pronotum short and broad; anterior lateral and anterior borders making a continuous broad circle from the shoulders; posterior lateral borders short; posterior border straight. Mesonotum large. Face strongly inflated. Tegmina coriaceous, venation fairly regular, rather indistinct with three ante-apical and four apical cells; claval veins nearly straight and parallel. Legs rather short and stout; anterior tibiae with numerous rather long stout spines on the posterior border. Hind tibiae half again as long as the posterior femora.

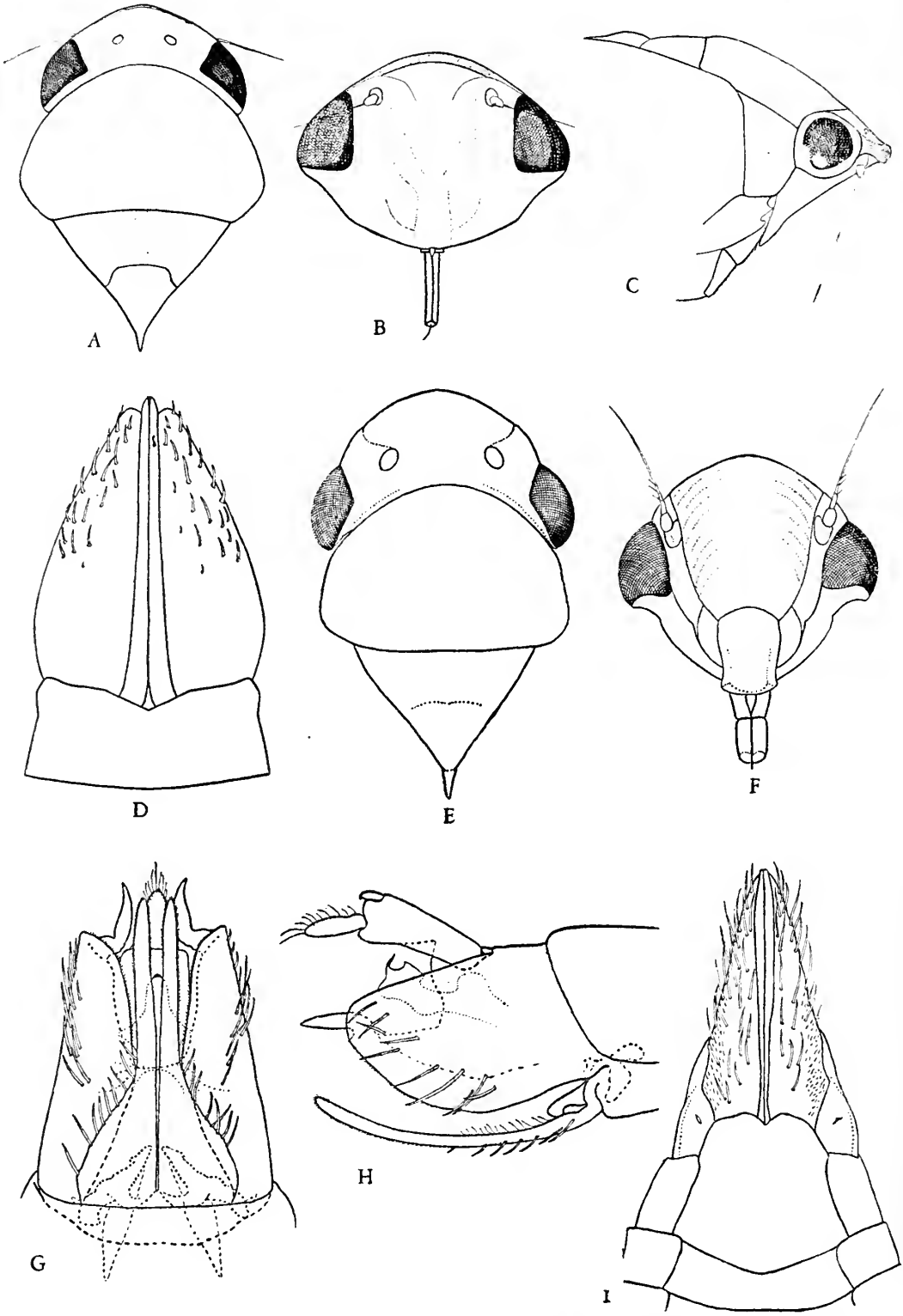
**Scarisana variabilis** n. sp.

(Text-fig. 8 E-I).

This is a variable species as far as color is concerned. Some specimens are light ochraceous buff, others are deep tawny.

Crown rather long and broad, nearly twice as wide as the median length; anterior margin broadly parabolic. Ocelli behind the middle farther from each other than from the compound eyes. Pronotum about one and one-half times as broad as its median length; anterior lateral and anterior borders broadly curved; posterior border nearly straight. Mesonotum large, broader than long. Apex produced into a distinct spine-like process.

Female last ventral segment about four times as long as the penultimate with a distinct V-shaped notch on the posterior border. Male genitalia with genital plates broad at the base, gradually restricted to near the




TEXT-FIG. 8. *Marganalana testacea*: **A**, head thorax; **B**, face; **C**, head thorax lateral; **D**, female genitalia. *Scarisana variabilis*: **E**, head thorax; **F**, face; **G**, male genitalia ventral; **H**, male genitalia lateral; **I**, female genitalia.

middle then nearly parallel to the apex. Pygofers with a distinct apical process.

Length to apex of tegmina: 11.25 mm.

Holotype ♂: British Guiana.

Allotype ♀: Kartabo, Bartica District, British Guiana.

Paratypes 3 ♂♂, Kartabo, Bartica District, British Guiana, various dates. 4 ♀♀ Kartabo, Bartica District, British Guiana, various dates.

**Scaris** Le Peletier and Serville, 1825a:609.

Haplotype *Iassus ferrugineus* Fabr.

This genus is unknown to me. I repeat below the more essential portions of the original description, as there is no modern description. Germar, 1833a:179, separated it from his new genus *Gypona* as having the ocelli remote from each other, whereas in *Gypona* the ocelli are approximate. Subsequent authors added but little. Evans, 1947a:215; fig. 30 G, has an excellent illustration of the head and thorax of the species *Scaris ferruginea* Fabr.

Body somewhat triangular. Crown short, transverse, much narrower than the pronotum but of the same width as the anterior margin of the pronotum, with anterior border of the head thick, rounded. Ocelli remote from each other. Pronotum not dilated laterad, transverse, rather long, narrowed anteriorly and also a little posteriorly, truncate on posterior margin. Mesonotum triangular, prolonged caudad into an elongate sharp process.

## Literature Cited.

All references to the literature in this paper are cited by author and date according to the references in the author's *Bibliography of the Homoptera* (1942) except the articles which have been published since that time.

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Names in **bold face** indicate new genera, species or varieties; numbers in **bold face** indicate illustrations; numbers in parentheses are the serial numbers of papers containing the plates listed immediately following.

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